Generic Revision of the Neogastropod Family Pseudolividae

Geerat J. Vermeij

Department of Geology and Center
    for Population Biology
University of California at Davis
Davis, CA 95616 USA
vermeij@geology.ucdavis.edu

ABSTRACT

The neogastropod family Pseudolividae Cossmann, 1901, is a Late Cretaceous to Recent group of about one hundred species characterized by a spiral groove (pseudolivid groove) on the lower half of the last whorl, a labral tooth on the outer lip at the end of this groove, a posterior notch at the adapical end of the outer lip, spiral sculpture increasing in prominence toward the base, and an indeterminate, sharp-edged, planar outer lip. A genus-level revision based on shell characters supports previous anatomical studies in recognizing the Pseudolividae as a taxon distinct from other neogastropod families.

I recognize fourteen genera in the Pseudolividae: *Benthobia* Dall, 1889 (Recent, low-latitude bathyal and abyssal oceans); *Fulmentum* Fischer, 1884 (Recent, West and South Africa); *Fusopsis* Ravn, 1939 (Paleocene, Denmark); *Fusulculus* Bouchet & Vermeij, 1997 (Recent, New Caledonia); *Hubachia* Etayo Serna, 1979 (Paleocene, Colombia); *Luizia* Douvillé, 1933 (Early Miocene to Recent, West Africa); *Macron* H. & A. Adams, 1853 (Early Miocene to Recent, warm-temperate North Pacific and Caribbean); *Naudoliva* Kilburn, 1989 (Recent, southeastern Africa); *Pseudoliva* Swainson, 1840 (Early Miocene to Recent, West Africa); *Sulcobuccinum* d'Orbigny, 1850 (Late Cretaceous (Campanian) to Early Oligocene, warm seas worldwide); *Sulcoliva*, new genus (type species: *Pseudoliva monilis* Olsson, 1928; Eocene, Peru); *Testallium* Vermeij & DeVries, 1997 (Early Miocene to Late Pliocene, western South America); *Triumphis* Gray, 1857 (Early Miocene?, Recent, tropical eastern Pacific); and *Zemira* H. & A. Adams, 1853 (Late Eocene to Recent, Australia). I designate *Buccinum fissuratum* Deshayes, 1835, the type species of *Sulcobuccinum*, of which the following taxa are subjective junior synonyms: *Buccinorbis* Conrad, 1865; *Calorebama* Squires, 1989; *Pegocomptus* Zinsmeister, 1983; and *Popenoeum* Squires, Zinsmeister & Paredes-Mejia, 1989. The genus *Sylvanocochlis* Melvill, 1903, is a junior subjective synonym of *Fulmentum*. *Pseudoliva guppyi* Mansfield, 1925, from the Late Miocene of Trinidad, is assigned to *Fusulculus* with great hesitation. I propose *Sulcobuccinum multinodulosum* as a replacement name for *Pseudoliva chavani* Glibert, 1973, *non* Tessier, 1952. *Macron mcleani* is a new species described from the Recent fauna of the Gulf of California.

Genera removed from Pseudolividae include *Austrosphaera* Camacho *in* Furque & Camacho, 1949 (Late Cretaceous to Paleocene, Argentina); *Seymourosphaera* Oleinik & Zinsmeister, 1996 (Early Paleocene, Seymour Island, Antarctic Peninsula); and the Late Cretaceous genera *Fulgerca* Stephenson,

1941, *Hydrotribulus* Wade, 1916, and *Ptychosyca* Gabb, 1877, all from the Gulf Coastal Plain of the United States. These taxa are not reassigned to other families, but belong to basal buccinoids. *Nicema* Woodring, 1964, which has sometimes been considered a subgenus of *Triumphis*, is a Late Miocene to Recent tropical American genus here assigned to the buccinid subfamily Photinae. The Pliocene to Recent South African genus *Melapium* H & A. Adams, 1853, may belong to the largely Paleogene family Streptturidae.

Key words: Muricoidea, Psuedolividae.

INTRODUCTION

The Pseudolividae is a distinctive family of some one hundred species of neogastropods, whose origin can be traced to the Late Cretaceous. The history of this family contrasts markedly with that of many other neogastropod families including the Muricidae, Fasciolariidae, Cancellariidae, Mitridae, and Conidae, which likewise originated during Late Cretaceous times (Taylor et al., 1980; Bandel, 1993). Whereas these latter families underwent spectacular phases of diversification during both the Paleogene and Neogene, the Pseudolividae have declined in diversity and geographical range since their peak during the Paleogene. The group is represented today by only about sixteen species, a number that is one to two orders of magnitude smaller than the living diversity in each of the other families.

In order to understand why some clades diversified during the Neogene while others dwindled in diversity, we must specify the order and timing of evolutionary branching events, as well as the ecological and geographical context of evolution and extinction in the contrasting groups. Such a phylogenetic understanding, in turn, hinges critically on a comprehensive account of the taxonomy of the groups in question.

The aim of this paper is to present a taxonomic review of all genera of Pseudolividae and to reassign genera that have been previously referred to the Pseudolividae or that were considered to belong to genera here assigned to that family. In the second part of the study (Vermeij & Carlson, in preparation), we present a phylogeny of

the group together with a narrative evolutionary and bio-geographical history of the Pseudolividae.

PREVIOUS WORK

A comprehensive genus-level review of the Pseudolivi-dae has not been attempted in more than fifty years. Cossmann (1901), Thiele (1929), and Wenz (1938–44) compiled the genera of the group, but they did not crit-ically evaluate the limits of the taxa they recognized, and assigned most members of the Pseudolividae to the type genus *Pseudoliva*. Adegoke (1977) recognized the diver-sity of Paleocene and Eocene pseudolivids was too great to be accommodated in the genus *Pseudoliva* and its subgenus *Buccinorbis*, but he declined to propose new superspecific taxa. Although some of these groups were subsequently named (Zinsmeister, 1983; Squires, 1989; Squires et al., 1989), the naming of fossil members of the family proceeded piecemeal, and several superspe-cific taxa named earlier were overlooked. With the exception of Ponder and Darragh's (1975) paper on *Zemira*, which treated fossil as well as living species, most studies of Recent pseudolivids did not incorporate data on fossil forms.

Varying interpretations of the phylogenetic position of the Pseudolividae have contributed to confusion sur-rounding the taxonomic assignment of several genera, as well as to difficulties in defining the limits of the family. Perhaps because *Pseudoliva* has a smooth shell superfi-cially resembling some members of the Olividae, many twentieth-century authors followed Swainson (1840) in placing *Pseudoliva* in or near the Olividae (see e.g. Mel-vill, 1903; Thiele, 1929; Wenz, 1938–44; Glibert, 1960; Taylor & Sohl, 1962; Sohl, 1964a, b; Ponder & Darragh, 1975; Adegoke, 1977; Ponder & Warén, 1988; Kilburn, 1989). Strongly sculptured genera such as *Luizia*, *Ma-cron*, and *Triumphis* were therefore not recognized as pseudolivids, and were instead referred to the Buccini-dae (Thiele, 1929; Douvillé, 1933; Wenz, 1938–44; Gli-bert, 1963; Addicott, 1970; Keen, 1971; Abbott, 1974).

In their treatment of gastropod genera, H. & A. Ad-ams, (1853) assigned their new genus *Zemira*, together with *Pseudoliva* and its new subgenus *Macron*, to the muricid subfamily Purpurinae, a taxon encompassing genera that are assigned by modern authors to the mur-icid subfamilies Rapaninae and Ocenebrinae (see e.g. Kool, 1993; Vermeij & Kool, 1994; Vermeij, 1995; Ver-meij & Vokes, 1997; Vermeij & Carlson, in preparation). This assignment was supported by characters of the rad-ula and by the mistaken assertion that the opercula of these genera have a lateral nucleus, as do many muri-cids. Beyrich (1854) referred two small Lattorfian (= Priabonian, latest Eocene) species from North Germany to the genus *Purpura*, but he did not comment on his reasons for this assignment. One of these species, *P. pus-illa*, was thought by Beyrich to lack the characteristic pseudolivid groove. Von Koenen (1889) referred the two species to *Pseudoliva*, pointed out that both exhibited

the characteristic groove, and maintained that they have little in common with *Purpura*.

Sowerby (1846) was the first author to propose a close relationship between *Pseudoliva* and the Buccinidae. He considered *Pseudoliva* to be closely related to *Eburna* Lamarck, 1822 (non Lamarck, 1801), the buccinid genus known today as *Babylonia* Schlüter, 1838. Cossmann (1901) considered the Pseudolivinae as a subfamily of Buccinidae and included in it *Pseudoliva*, *Buccinorbis*, and *Fulmentum*; but he assigned *Zemira* and *Macron* to the Latrunculinae (= Babyloniinae) and *Triumphis* to the Cominellinae (= Photinae). Assignment of *Pseudo-liva*, its subgenus *Buccinorbis*, and related Paleogene genera to the Buccinidae or Buccinoidea was accepted by von Koenen (1889), Fischer (1884), Böhm (1926), Palmer (1937), Gardner (1945), Golikov & Starobogatov (1975), Dockery (1977, 1880), and Squires (1989), among others. Shell characters formed the basis for most of these assignments.

Kantor's (1991) anatomical and phylogenetic study provided strong support for separating the Psendolividae as a distinct family from other oliviform gastropods (see also Kantor, 1996). He isolated the group in a new sub-order Pseudolivoidei, which together with the Muricoid-ei comprises the order Rachiglossa. Many derived fea-tures in Olividae, including pedal lobes, inner-whorl re-sorption, posterior mantle tentacle, mobile crescent-shaped propodium, and absence of the operculum, for example, are absent in Pseudolividae. Character states of Pseudolividae interpreted to be plesiomorphic for neogastropods include position of radular sac at base rather than near tip of proboscis, and (in *Benthobia*) the connection between the radular retractor muscle and the columellar muscle. In Pseudolividae, the proboscis is formed by elongation of the buccal tube, and there is a well defined Gland of Leiblein; whereas in the Muri-coidei, which includes the Olividae and Buccinidae, the proboscis is formed by the elongation of the dorsal wall of the buccal cavity (Kantor, 1991).

The present study is based on shell characters. Many authors dismiss shell characters as unreliable for infer-ring phylogeny above the species level on the grounds that the shell is more subject to environmental variation and to evolutionary convergence than are the animal's internal organs. Not only is this argument predicated on untested and probably false assumptions, but it also ef-fectively eliminates phylogenetic assessments of fossil forms. There can be no question that data on anatomy and on DNA sequences are immensely valuable in con-structing classifications and phylogenies of living species; but they have only limited power in helping paleontol-ogists make sense of the diversity of shells encountered in the fossil record. Instead of ignoring shell characters, we should evaluate the latter carefully. The aim of the present study is therefore to present a unified scheme of classification of both living and fossil pseudolivids based on a detailed analysis of shells.

MATERIALS AND METHODS

I have examined the type species of all but two genera of the Pseudolividae, as well as many additional species within and outside the family. A complete list of recognized species of Pseudolividae, together with material examined, is given in Appendix 1. Material of species discussed in this paper but not belonging to the Pseudolidae is listed in Appendix 2.

ABBREVIATIONS

ANSP   Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
BMNH   The Natural History Museum, London, UK
CAS   California Academy of Science, San Francisco, California, USA
IGPS   Institute for Geology and Paleontology, Tohoku University, Sendai, Japan
IRSNB   Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
LACM   Los Angeles County Museum of Natural History, Los Angeles, California, USA
MNHN   Muséum national d'Histoire naturelle, Paris, France
MGS   Mississippi Geological Survey, Jackson, Mississippi, USA
NM   Natal Museum, Durban, South Africa
PU   Purdue University, West Lafayette, Indiana, USA
PRI   Paleontological Research Institute, Ithaca, New York, USA
RGM   Nationaal Museum voor Natuurlijke Historie, Leiden, The Netherlands
SAM   South African Museum, Capetown, South Africa
SGO PI Museo Nacional de Chile, Instituto de Palontologia, Santiago, Chile
TMM   Texas Memorial Museum, Austin, Texas, USA
UCMP   University of California Museum of Paleontology, Berkeley, California, USA
USNM   United States National Museum of Natural History, Washington, DC, USA
GJV   Vermeij collection
YPM   Yale Peabody Museum, New Haven, Connecticut, USA

SYSTEMATICS

Class Gastropoda
Subclass Prosobranchia
Order Neogastropoda
Superfamily Muricoidea Rafinesque, 1815
Family Pseudolividae Fischer, 1884

Diagnosis: Shell very small to large, maximum height 5 to 100 mm, ovate to fusiform; spire consisting of six or fewer teleoconch whorls; last whorl comprising 60% or more of total shell height; spiral sculpture usually present, consisting of a deep groove (pseudolivid groove) on basal half of last whorl, and of cords or threads that increase in degree of expression abapically; axial sculpture, when present, consisting of eight or more ribs per whorl, restricted to upper part of whorl; outer lip thin, sharp at edge, the adaxial layer not reflected over the edge to the abaxial side; pseudolivid groove terminating at edge of outer lip in blunt or sharp, ventrally directed tooth (labral tooth); outer lip often crenulated below labral tooth by terminations of grooves between basal cords; edge of outer lip planar, without sinuses except for adapical notch where outer lip joins penultimate whorl; inner lip smooth, adherent throughout its length to penultimate whorl, weakly concave, sometimes with weak fold at entrance of siphonal canal, sometimes with parietal tooth at adapical end; columellar and parietal callus variably expressed; living species with persistent periostracum.

Included genera: *Benthobia* Dall, 1889; *Buccinorbis* Conrad, 1865; *Fulmentum* Fischer, 1884; *Fusopsis* Ravn, 1939; *Fusulculus* Bouchet & Vermeij, 1997; *Luizia* Douvillé, 1933; *Hubachia* Etayo Serna, 1979; *Macron* H. & A. Adams, 1853; *Pseudoliva* Swainson, 1840; *Sulcobuccinum* d'Orbigny, 1850; *Sulcoliva* new genus; *Testallium* Vermeij & DeVries, 1997; *Triumphis* Gray 1857; *Zemira* H. & A. Adams, 1853.

Stratigraphic range: Late Cretaceous (Campanian) to Recent.

Discussion: *Characters:* None of the shell characters of the Pseudolividae is by itself unique to the family, but the constellation of characters serves to set the group apart from other neogastropod clades. Perhaps the most distinctive feature of the Pseudolividae is the so-called pseudolivid groove, a spiral depression on the lower part of the whorl that terminates in a ventrally and often adaxially projecting tooth (labral tooth) on the outer edge of the outer lip. The groove and tooth are obsolete in *Benthobia* and *Macron lividus*, and absent in *Triumphis*.

A labral tooth at the end of a groove is not unique to the Pseudolividae. It has also evolved numerous times in the Muricidae (many members of the subfamilies Muricinae, Ocenebrinae, and Rapaninae), Buccinidae (Pisaniinae of the genus *Cantharus* Röding, 1798, and related taxa; and Siphonaliinae of the Eocene genus *Phoracanthus* Cossmann & Martin *in* Martin, 1914), Echinofulgurinae (members of the genera *Cornulina* Conrad, 1853, and *Protobusycon* Wade, 1917), Fasciolariidae (the genus *Opeatostoma* Berry, 1958), Turbinellidae (the genus *Ceratoxancus* Kuroda, 1952), Olividae (many members of the subfamily Ancillinae), and various other buccinoids such as the Cretaceous genera *Buccinopsis* Conrad, 1857, and *Odontobasis* Meek, 1876, as well as the Recent *Tritonidea dentata* Schepman, 1911 (see e.g. Sohl, 1964a, b; Bouchet & Warén, 1985; Vignon, 1931; Vokes, 1990, 1992; Vermeij & Kool, 1994; Vermeij & Vokes, 1997; DeVries & Vermeij, 1997).

The simple, sharp-edged outer lip of fully grown

pseudolivids does not differ from that of ontogenetically younger individuals, and therefore indicates indeterminate growth according to the criteria set out by Vermeij and Signor (1992). The adult outer lip of *Triumphis* and of several large Eocene species of *Sulcobuccinum* is often adapically more extended than is that of individuals at earlier stages of growth, so that the spire comes to have a strongly concave lateral profile; but there is no evidence that growth in the spiral direction ceases at maturity, as would be the case in shells with determinate growth. Many pseudolivids (especially Eocene species of *Sulcobuccinum*) develop massive columellar and parietal callus deposits in adulthood, but again there is no evidence that growth at the outer lip ceases.

The indeterminate growth pattern of pseudolivids appears to be the plesiomorphic condition in neogastropods. It characterizes all Cretaceous buccinoids as well as Cenozoic Melongenidae, Turbinellidae, Fasciolariidae, Olividae (Ancillinae), and many clades within Muricidae, Buccinidae, and Conoidea, among others (see Vermeij & Signor, 1992).

The edge of the outer lip of Pseudolividae usually lies in a plane. Its contour is interrupted only by the emargination at the siphonal canal and by the adapical notch (see below). A planar outer lip also characterizes many Muricidae and Conidae. In many other neogastropods, the edge of the outer lip is medially convex downward, the convex sector being flanked adapically and sometimes abapically by a shallow, downwardly concave sinus. Variations on this more convex outer lip are found among Buccinidae, Mitridae, Costellariidae, Melongenidae, Nassariidae, Fasciolariidae, Turbinellidae, and many other groups.

In fully grown Pseudolividae, the smooth inner (adaxial) layer of the outer lip does not extend across the edge to the outer (abaxial) side. As a result, the edge is sharp and not glazed. This configuration occurs also in Muricidae, pisaniine Buccinidae, and Conidae, among others. The edge of the outer lip is polished smooth by the inner layer extending across it in most photine and babyloniine buccinids, nassariids, mitrids, and melongenids.

Nearly all members of the Pseudolividae are characterized by a posterior (or adapical) notch of the outer lip. This is an indentation where the outer lip joins the penultimate whorl at the adapical end of the aperture. A comparable notch occurs in many gastropods, including many muricine and rapanine muricids, columbellids, photine buccinids, melongenids, nassariids, mitrids, volutids, olivids, and conoideans. Within Pseudolividae, a few genera (*Benthobia, Fusulculus, Naudoliva,* and some large individuals of *Triumphis*) apparently lack a posterior notch.

Spiral sculpture in the Pseudolividae is usually better expressed on the lower part of the whorl than on the upper portion. As a result, crenulations at the ends of spiral grooves are most strongly expressed on the basal sector of the outer lip below the pseudolivid groove. This character state occurs widely among neogastropods

including Columbellidae, many Buccinidae (Siphonaliinae, Photinae), Nassariidae, many Fasciolariidae, Costelariidae, Mitridae, Harpidae, and many Conoidea. In some Melongenidae, this pattern is superimposed on a spiral sculpture of keels or folds that decrease in prominence toward the base. In muricids and in the buccinid subfamily Pisaniinae, the strongest spiral sculptural elements always occur on the upper part of the whorl near the shoulder, decreasing both toward the base and from the shoulder to the suture above.

In Pseudolividae bearing axial sculpture, the axial elements are confined to the part of the last whorl above the pseudolivid groove. The restriction of axial sculpture to the upper part of the whorl is very widespread in Cretaceous neogastropods (Sohl, 1964a, b), and also characterizes many clades in the Buccinidae, Fasciolariidae, Nassariidae, Columbellidae, and Conoidea, among others.

The inner lip of Pseudolividae is smooth and always adherent above the siphonal fasciole, that is, its edge merges imperceptibly with the outer surface of the preceding whorl on which the inner lip encroaches during growth. Even when a thick callus is formed on the inner lip, as in species of *Sulcobuccinum* and *Pseudoliva*, the abaxial edge of the callus is rarely distinct. A smooth, adherent inner lip also characterizes Melongenidae, basal Conoidea, and many groups within Buccinidae, Muricidae, and Fasciolariidae (Fusininae). In most Olividae, including the Ancillinae, the inner lip is sculptured by thin, often very numerous spiral riblets; but a smooth inner lip occurs in the ancilline genus *Eburna* Lamarck, 1801.

In most Pseudolividae, the columella terminates abapically in a simple point on the left (adaxial) side of the siphonal canal or notch. This condition is widespread in Cretaceous buccinoids as well as in Cenozoic Buccinidae (Buccininae, Volutopsiinae) and basal Conoidea. In the pseudolivids *Macron* and *Triumphis*, however, there is a weak fold on the columella at the upper entrance of the siphonal canal. The abapical end of the columella therefore appears truncated in these genera. A basal columellar fold is very widespread in neogastropods including Muricidae, Fasciolariidae, and many Buccinidae (Pisaniinae and Siphonaliinae), but the truncation observed in *Macron* and *Triumphis* is less common, being best known in the Nassariidae and the buccinid subfamily Photinae (see Allmon, 1990).

The protoconch in most pseudolivids is paucispiral, here defined as having fewer than three whorls. The only genera with a multispiral protoconch are *Benthobia* and *Fusopsis*. Multispiral protoconchs are extremely widespread among Cretaceous buccinoids, and likely represent the primitive state of neogastropods in general and of the Pseudolividae in particular.

Comparisons with other Neogastropods: Some Pseudolividae superficially resemble the Olividae in having a posterior (adapical) notch, a relatively smooth shell, a low spire, and thick callus deposits on the columellar and

parietal regions. Members of the olivid subfamily Ancillinae further resemble pseudolivids in usually having a basal spiral groove (ancillid groove) and corresponding labral tooth. The ancillid groove is formed at the adapical margin of a broad, flat, somewhat raised zone (ancillid band) which is situated above the siphonal fasciole and which lacks the spiral cords or threads characteristic of pseudolivids. The labral tooth of Ancillinae lies at the entrance of the siphonal canal, whereas in Pseudolividae it is situated a short distance above the entrance of the canal, from which it is separated by a short crenulated sector of the outer lip. Olividae further differ from Pseudolividae in having most or all of the shell covered with a callus glaze, which is deposited by pedal lobes that are absent in Pseudolividae (Kantor, 1991).

Gardner (1945) thought that the Eocene genus *Ancillopsis* Conrad, 1865 (type species: *Ancillaria altilis* Conrad, 1832) might be closely related to *Pseudoliva*. This genus is characterized by an ovate, smooth, basally unconstricted shell, by a smooth concave columella, a posterior notch, and a distinct fasciolar band, above which a spiral groove ends in a slight tooth-like or lobe-like protrusion at the outer lip. *Ancillopsis* differs from Pseudolividae by having the spire covered with a glaze of callus, by the absence of a pseudolivid groove, and by lacking spiral and axial sculpture. Allmon (1990) showed that *Ancillopsis* does not belong with *Bullia* Gray *in* Griffith & Pidgeon, 1834, in the nassariid subfamily Dorsaninae, where Palmer (1937) and Palmer and Brann (1966) had placed it, because it lacks the terminal columellar fold characteristic of Nassariidae. *Ancillopsis* may be a divergent member of the Ancillinae.

The family Strepturidae Cossmann, 1901, has occasionally been subsumed under, or synonymized with, the Pseudolividae (see e. g. Ponder and Warén, 1988). Based on the type genus *Strepsidura* Swainson, 1840 (type species: *S. turgida* (Solander *in* Brander, 1766), the Strepturidae have in common with the Pseudolividae the following characters: spiral sculpture increasing in prominence toward the base, axial sculpture most prominent on upper part of whorl, and presence of small adapical notch. The Strepturidae differ, however, by the absence of a pseudolivid groove and labral tooth, and by having the inner shell layer reflected slightly over the outer lip's edge, which is therefore smooth and polished. Unlike most Pseudolividae, the Strepturidae have a very strong fold on the columella at the entrance of the siphonal canal. The genus *Melapium* H. & A. Adams, 1853, has often been included in either the Strepturidae (Cossmann, 1901) or Pseudolividae (Thiele, 1929; Wenz, 1938–44; Kilburn, 1989). As discussed later in this paper, I tentatively support Cossmann's (1901) assignment of *Melapium* to the Strepturidae. If this proves to be correct, then the anatomical study of *Melapium* by Kantor (1991) would imply that the Strepturidae, which are known mainly from the Paleogene, are relatively primitive neogastropods related to the Olividae.

Several members of the Melongenidae bear a close resemblance in shell characters to the Pseudolividae.

Neogene to Recent genera such as *Melongena* Schumacher, 1817, and *Volema* Röding, 1798, share with pseudolivids a low-spired, indeterminately growing shell, a smooth columella without a basal fold, an adherent inner lip, a thick persistent periostracum, and a distinct adapical (posterior) notch in the outer lip. They differ from pseudolivids by lacking a basal groove and corresponding labral tooth as well as in the development of spiral sculpture. In melongenids, grooves ending in crenulations at the outer lip increase in prominence from the shoulder to the base, as in pseudolivids, but spiral keels or strong cords that often bear nodes or spines are most prominent on the upper part of the whorl.

In the Early Miocene (Aquitanian and Burdigalian) *Melongena lainei* (Basterot, 1825) from southwest France, the outer lip of the adult shell usually has a downwardly convex protrusion. In a few individuals, this protrusion, which corresponds to the basal constriction of the last whorl, bears a very weak, blunt labral tooth (for further discussion of this species see Peyrot, 1927; Vignon, 1931).

The genus *Cornulina* Conrad, 1853, contains several Late Paleocene and Eocene species with a "pseudolivid" groove and corresponding labral tooth. These include the type species, *C. minax* (Solander *in* Brander, 1766) from the Middle and Late Eocene of Europe and *C. armigera* (Conrad, 1833) from the Middle Eocene of the southeastern United States. Like members of the Pseudolividae, *Cornulina* is characterized by indeterminate growth, a sharp-edged outer lip, adherent smooth inner lip, and outer-lip crenulations that become more pronounced abapically. It differs from Pseudolividae by the absence of an adapical notch and by the presence of two prominent spiral rows of nodes, and from Eocene pseudolivids by the presence of a parietal rib and a basal columellar fold. Petuch (1994) interpreted *Cornulina* as an ancestor, or an early member of his subfamily Echinofulgurinae of the family Melongenidae. The earliest undoubted *Cornulina*, *C. praecursor* Cossmann, 1902, dates from the Thanetian stage of the Late Paleocene of the Paris Basin in France.

Protobusycon Wade, 1917, may be an even earlier genus in this group. The two Late Cretaceous members of this genus from the Gulf Coastal Plain of the United States (see Sohl, 1964a) bear a labral tooth at the end of a groove on the lower part of the last whorl. Suggestions that *Protobusycon* (type species: *Busycon cretaceum* Wade, 1917) belongs to the Turbinellidae (Bandel, 1993) or Ficoidea (Riedel, 1994) seem far-fetched. Turbinellids (especially Paleogene species) lack the parietal rib characteristic of *Protobusycon*. Ficoids, which Riedel (1994) argues are basal neogastropods, have internal shells without a labral tooth. The spines or nodes on the upper part of the whorl of *Protobusycon* indicate that the shell was probably external. Like *Cornulina*, *Protobusycon* differs from Paleogene pseudolivids by the presence of a parietal rib and the absence of a posterior notch. In contrast to the situation in Pseudolividae, axial sculpture in *Protobusycon* extends to the siphonal canal,

which is very long. Spiral sculpture generally decreases in strength adapically on the last whorl of *Protobusycon* as it does in pseudolivids, but two widely separated rows of nodes (one at the shoulder and one just above the tooth-bearing groove) are superimposed on this pattern, as they are in *Cornulina*. The single Paleocene species of *Protobusycon* (*P. judithae* Saul, 1988, from the "Martinez" stage of California) may not have possessed a labral tooth, but the genus could nonetheless have given rise to, or be the sister group of, *Cornulina*. In any case, the labral tooth of this group probably evolved independently from that in the Pseudolividae.

The genus *Lacinia* Conrad, 1853, comprises Middle Eocene shells remarkably similar in form to contemporaneous species of the pseudolivid genus *Sulcobuccinum* (see below). Like *Sulcobuccinum*, *Lacinia* has a low-spired, ovate, basally unconstricted, thick, indeterminately growing shell with a distinct adapical notch and extensive columellar and parietal callus. *Lacinia alveata* (Conrad, 1833) from the Gosport Sand (Middle Eocene) of Alabama, the type species of *Lacinia*, is a large species (maximum height 115 mm) characterized by a ventral protrusion on the outer lip about one-third the distance from the base of the shell. This protrusion corresponds to a very shallow, very broad spiral depression on the last whorl. Below this protrusion, the outer lip is finely crenulated. Unlike Paleogene pseudolivids, *Lacinia* has a distinct fold at the base of the columella. Moreover, this spiral sculpture is better expressed on the upper part of the whorl, where it consists of four broad, rounded folds. *Lacinia* is represented by two species in the Gosport Sand of Alabama, *L. alveata* and the much smaller *L. claibornensis* Palmer, 1937, a species with axial ribs on the spire whorls. Vredenburg (1922) has named three species of *Lacinia* from the Late Eocene and Oligocene of Burma and India. The Late Eocene Nigerian *Athleta lugardi* Newton, 1922, the type of *Laccinum* Eames, 1957, is very similar to *Lacinia* except that it lacks any trace of spiral sculpture.

Palmer (1937) and Wenz (1938–1944) assigned *Lacinia* to the Buccinidae, but the genus could equally well be included in the Melongenidae. It is even possible that *Lacinia* and *Laccinum* are divergent members of the Pseudolividae. For the time being, I consider their taxonomic placement uncertain.

There is also a considerable resemblance in shell characters between Pseudolividae and the buccinid subfamily Babyloniinae, as exemplified by the Eocene to Recent genus *Babylonia* Schlüter, 1838 (type species: *B. spirata* (Lamarck, 1822)). Like many Pseudolividae, *Babylonia* is characterized by a thick periostracum, canaliculate suture, relatively low spire, planar simple outer lip, a posterior notch, a well developed siphonal fasciole, smooth columella without basal fold, and a basally unconstricted last whorl. *Babylonia* differs from Pseudolividae by having the glossy inner (adaxial) layer of the outer lip reflected over the edge of the outer lip, so that the edge is smooth and polished rather than sharp; and by lacking

basal spiral sculpture as well as a pseudolivid groove and labral tooth.

Members of the buccinid subfamily Pisaniinae have in common with pseudolivids a short spire, adherent periostracum, sharp-edged outer lip, smooth columella, and axial sculpture that is most strongly developed on the upper part of the whorl. Pisaniines differ from pseudolivids by having the spiral sculpture increasing in prominence from the base to the shoulder (adapically) rather than from the shoulder to the base (abapically), by having the edge of the outer lip ventrally convex instead of planar, and by lacking a posterior notch. Some Pisaniinae, such as the genera *Cantharus* Röding, 1798, and *Pollia* Gray *in* Sowerby, 1833, have a small labral tooth at the end of a spiral groove on the lower half of the last whorl, but this groove is a derived feature in the Pisaniinae and is therefore convergent with the labral tooth and groove of pseudolivids.

Shells of the buccinid subfamilies Photinae and Siphonaliinae differ from those of pseudolivids by having the edge of the outer lip polished rather than sharp in the fully grown shell, and usually by having a basal concave sector or sinus on the outer lip. Above this sinus, the outer lip of these buccinids is medially convex, and there is commonly a broad posterior sinus on the outer lip above the level of the shoulder. Some members of the Photinae, such as *Northia*, have a posterior notch at the upper end of this sinus. The siphonaliine genus *Phoracanthus* Cossmann & Martin *in* Martin, 1914 (type species: *Siphonalia ickei* Martin, 1914; Nanggulan beds, Eocene of Java) has a basal spiral groove ending in a labral tooth. Sculpture consists of fine spiral threads bundled into cords, and of widely spaced axial ribs on the upper part of the whorl (see Martin, 1914). It is likely that the labral tooth of *Phoracanthus* is convergent with that of Pseudolividae. A few species of Photinae also have a labral tooth. They include members of the genera *Cominella* Gray, 1850 (type species: *Cominella maculosa* (Martyn, 1784)) and *Iosepha* Tenison-Woods, 1879 (type species: *I. tasmanica* Tenison-Woods, 1879). In *Cominella acutinodosa* (Reeve, 1846) from Western Australia, a labral tooth is situated at the end of an enlarged central cord on the last whorl. In *Iosepha tasmanica* from southern Australia and *I. glandiformis* (Reeve, 1846) from New Zealand, a blunt labral tooth is formed at the center of the convex sector of the outer lip and does not correspond with either a cord or a groove. These labral protrusions are therefore not homologous with those of Pseudolividae.

Finally, the Muricidae differ from the Pseudolividae by having the spiral sculpture increasing in prominence from the base to the shoulder rather than from the shoulder to the base, and (in Paleogene forms) by lacking a posterior notch. In early muricids, moreover, axial sculpture almost always extends from the suture to the base, and is not confined to the upper part of the whorl. No muricids have the thick, persistent periostracum typical of pseudolivids.

KEY TO GENERA OF PSEUDOLIVIDAE

1a Protoconch multispiral (three whorls or more)
. . . . 2

1b Protoconch paucispiral (less than three whorls)
. . . . 3

2a Shell fusiform, relatively slender (height-to-diameter ratio 2.0); spiral sculpture consisting of fine cords . . . . *Fusopsis*

2b Shell inflated (height-to-diameter ratio 1.4 to 1.6); spiral sculpture obsolete . . . . *Benthobia*

3a Inner (adaxial) side of outer lip lirate (bearing spiral riblets) 4

3b Inner side of outer lip smooth or unknown . . . 6

4a Shell moderately slender (height-to-diameter ratio 1.7 to 1.9); axial sculpture present on upper part of whorls; parietal rib absent; abapical end of columella pointed . . . . *Luizia*

4b Shell relatively broad (height-to-diameter ratio 1.4 to 1.8); axial sculpture absent or confined to early whorls; parietal rib present; abapical end of columella with distinct fold 5

5a Pseudolivid groove and labral tooth absent; axial sculpture present on early whorls; outer lip adapically extended at maturity . . . . . . *Triumphis*

5b Pseudolivid groove and labral tooth present (but obsolete in *Macron lividus*); axial sculpture absent; outer lip not adapically extended at maturity . . . . *Macron*

6a Pseudolivid groove situated low on last whorl; parietal rib present 7

6b Pseudolivid groove situated high on last whorl; parietal rib absent 9

7a Spiral sculpture present on whole surface of last whorl; axial sculpture present on early whorls, or expressed as strong growth lines on last whorl; columellar callus thin, of limited extent . . . . *Testallium*

7b Spiral sculpture on last whorl absent; axial sculpture absent; columellar callus thick, extensive 8

8a Parietal rib rounded, not markedly constricting adapical end of aperture . . . . *Pseudoliva*

8b Parietal rib lamella-like, sharp-edged, separating long adapical channel from rest of aperture . . .
. . . . *Fulmentum*

9a Siphonal fasciole absent; siphonal notch very shallow 10

9b Siphonal fasciole present; siphonal notch deep . . 11

10a Suture linear, appressed; base of last whorl constricted; labral tooth obsolete; axial sculpture present on upper part of whorl . . . . . . *Fusulculus*

10b Suture deeply channeled; base of last whorl not constricted; labral tooth prominent; axial sculpture usually absent . . . . *Zemira*

11a Shell high-spired (last whorl comprising 60 to 70% of total shell height); pseudolivid groove indistinct; labral tooth present; last whorl constricted at base; columellar callus thin 12

11b Shell high-spired to low-spired; last whorl usually not constricted at base; pseudolivid groove and labral tooth distinct; columellar callus well developed, thick 13

12a Adapical notch absent; axial sculpture absent or consisting of short ribs at shoulder . . . *Naudoliva*

12b Adapical notch weak but present; axial sculpture consisting of narrow peripheral band of beads on last whorl . . . . *Sulcoliva*

13a Deep groove situated immediately below sharply angled shoulder; aperture very wide . . . . . .
. . . . *Hubachia*

13b Shoulder variably developed, without deep groove immediately below it; aperture narrower
. . . . *Sulcobuccinum*

Genus *Pseudoliva* Swainson, 1840
(Figures 10–12)

Type species: *Buccinum plumbeum* Chemnitz (= *Buccinum crassum* Gmelin, 1791) by monotypy.

Synonyms:
Gastridium Sowerby, 1842 (type species: *B. plumbeum* Chemnitz), *non* Modeer, 1793, *nec* Sowerby, 1846.

Diagnosis: Shell moderately large, maximum height 50 mm, ovate to globose; protoconch paucispiral; spire moderately low to very low, last whorl comprising 78 to 90% of total shell height; last whorl rounded above, not constricted basally; spiral sculpture confined to early teleoconch whorls, absent on last whorl; axial sculpture absent; pseudolivid groove situated low on last whorl; outer lip with distinct labral tooth, without basal crenulations; inner side of outer lip smooth; posterior notch deep; aperture ovate, its height-to-breadth ratio 2.1; columellar and parietal callus moderately thick, well developed ventrally, but not extending onto spire; parietal rib strong, rounded; siphonal fasciole low, rounded; anterior notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Early? Miocene, Madeira; Early Pliocene to Recent, southern Africa.

Discussion: Although Swainson (1840: 82, 306) proposed the name *Pseudoliva* for the West African species we know today as *Pseudoliva crassa* (Gmelin, 1791), *Pseudoliva* was interpreted broadly by paleontologists, who included in it a diverse array of gastropods with a basal groove and corresponding labral tooth. I follow Kilburn (1989) in restricting *Pseudoliva* to a small group of warm-temperate to subtropical West African species characterized by a non-umbilicate, smooth or obsoletely spirally threaded, ovate shell with a posterior notch, parietal rib, well developed callus, and smooth inner (adaxial) side of the outer lip. *Pseudoliva* differs from *Sulcobuccinum* by having the pseudolivid groove and labral tooth situated lower on the whorl, by the presence of a rounded parietal rib at the adapical end of the inner lip, and by being essentially smooth, there being no trace of

axial sculpture. *Sulcobuccinum kitsoni* (Newton, 1922) from the Ameki Formation (Middle Eocene) of Nigeria shows a trace of the parietal rib, and may be transitional between *Sulcobuccinum* and *Pseudoliva*. In the related genus *Fulmentum*, the parietal rib has become exaggerated as a plate, which sets a long, channel-like adapical section off from the rest of the aperture. *Pseudoliva* differs from *Testallium* by lacking spiral sculpture on the last whorl and by not having the last whorl constricted at the base.

I recognize three species in the genus *Pseudoliva* (see Appendix). The type species, *P. crassa*, is known only from the coast of Angola. The largest specimen I have seen (height 49.0 mm) comes from the Baia dos Tigres. Kensley and Pether (1986) described a very closely related if not identical form as *Pseudoliva lutulenta* from the 50 m level (Early Pliocene; J. Pether, personal communication) at Hondeklip, on the west coast of South Africa. The earliest member of the genus appears to be *P. orbignyana* Mayer, 1864, from deposits of probably Early or Middle Miocene age on Madeira.

Kilburn (1989) synonymized *Sylvanocochlis* Melvill, 1903, with *Pseudoliva*. Its type species, *Pseudoliva ancilla* Hanley, 1859, from the Agulhas Bank off South Africa, differs from *Pseudoliva* by its high spire and adapically extended aperture. As discussed below under *Fulmentum*, I consider *Sylvanocochlis* a synonym of *Fulmentum*.

Genus *Fulmentum* Fischer, 1884

Type species: *Buccinum sepimentum* Rang, 1832.

Synonym:
Sylvanocochlis Melvill, 1903 (type species: *Pseudoliva ancilla* Hanley, 1859).

Diagnosis: Shell of moderate size, maximum height 40 mm, ovate; spire moderately low, last whorl comprising 75 to 88% of total shell height; last whorl evenly rounded above, weakly or not constricted basally; spiral sculpture usually absent, sometimes expressed as very weak threads below pseudolivid groove; axial sculpture absent; pseudolivid groove situated low on last whorl; outer lip with distinct labral tooth, below which small crenulations may appear; inner side of outer lip smooth; posterior notch present; aperture ovate (*F. sepimentum*) to elongate-ovate (*F. ancilla*), its height-to-breadth ratio 2.4 to 3.0; adapical end of aperture extended as narrow channel between outer lip and a prominent, projecting, plate-like parietal ridge at posterior end of inner lip; columellar and parietal callus well developed ventrally, but not extending onto spire; siphonal fasciole low, rounded, sculptured by five weak spiral threads; anterior siphonal notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Recent, tropical West Africa and temperate South Africa.

Discussion: Fischer (1884: 632) introduced *Fulmentum* as a subgenus of *Macron* for *Buccinum sepimentum*

Rang, 1832, a Recent species from tropical West Africa. Most later authors have treated *Fulmentum* as a full genus or as a subgenus of *Pseudoliva*. The exaggerated, plate-like parietal ridge, which sets apart a narrow adapical extension from the rest of the aperture, readily distinguishes *Fulmentum* from *Pseudoliva*. *Fulmentum sepimentum* ranges from Cotonou (Togo) to southern Angola. The largest specimen I have seen (height 20.4 mm) is from Pointe Noire, Congo (MNHN).

Melvill (1903: 325) named the genus *Sylvanocochlis* for *Pseudoliva ancilla* Hanley, 1859, a relatively large (maximum height 40 mm), high-spired species from the Agulhas Bank off South Africa. Kilburn (1989) considered *Sylvanocochlis* a synonym of *Pseudoliva*, correctly pointing out that spire height in *Pseudoliva* is quite variable and therefore an unreliable criterion for the recognition of genera. My examination of *Pseudoliva ancilla* prompts me to assign this species to *Fulmentum*. Like *F. sepimentum*, the South African species has a drawn-out adapical extension of the aperture, set off from the abapical main portion of the aperture by a flange-like parietal lamella. *Fulmentum ancilla* differs from *F. sepimentum* by being about twice as large and by not being constricted basally.

Genus *Sulcobuccinum* d'Orbigny, 1850

Type species: *Buccinum fissuratum* Deshayes, 1835, here designated (Figures 1–3).

Synonyms:
Buccinorbis Conrad, 1865 (type species: *Buccinum vetustum* Conrad, 1833, subsequent designation by Cossmann, 1901; Figures 5–7).
Pegocomptus Zinsmeister, 1983 (type species: *Molopophorus howardi* Dickerson, 1914, by original designation).
Calorebama Squires, 1989 (type species: *Pseudoliva dilleri* Dickerson, 1914, by original designation).
Popenoeum Squires, Zinsmeister & Paredes-Mejia, 1989 (type species: *Popenoeum maritimus* Squires, Zinsmeister & Paredes-Mejia, 1989, by original designation).

Diagnosis: Shell very small to large, maximum height 4.2 to 66 mm, ovate to globose; protoconch paucispiral; spire relatively high to low, last whorl comprising 63 to 100% of total shell height; last whorl rounded or shouldered above, usually not constricted at base; spiral sculpture variably expressed; axial sculpture consisting of eight or more ribs per whorl, confined to part of whorl above pseudolivid groove, and often forming nodes or spines at shoulder and at intersections with spiral cords; axial sculpture confined to spire whorls in some species; pseudolivid groove at relatively high position, not less than one-fourth from abapical end of last whorl; outer lip with distinct labral tooth, below which are three to five crenulations corresponding to grooves between basal cords; inner side of outer lip smooth; posterior notch present; aperture ovate to ovate-elongate, its height-to-breadth ratio 2.0 to 3.8; columellar and parietal callus variably expressed, often thick and extending onto spire in large Eocene species; parietal ridge absent; siphonal
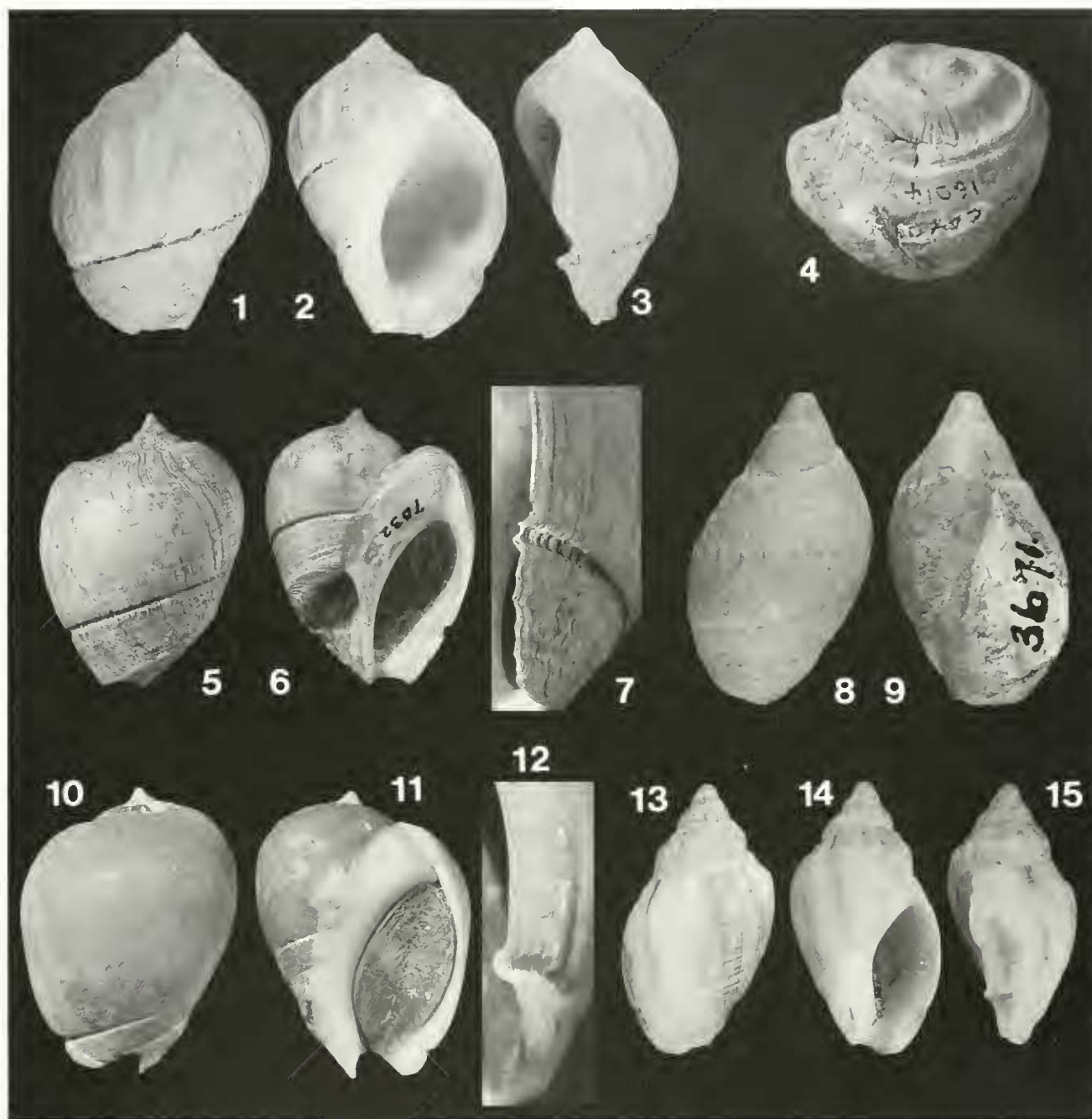
Figures 1–3. *Sulcobuccinum fissuratum* (Deshayes, 1835); Chàlons-sur-Vesle, Marne, France; Thanetian; MNHN. Shell height 38 mm.

Figure 4. *Hubachia ramirolobae* Etayo Serna, 1979, Paleocene, Colombia; UCMP 16014. Oblique view of apex; total shell height 30 mm

Figures 5–7. *Buccinorbis vetusta* (Conrad, 1865); Little Stave Creek, Alabama; Gosport Sand (Middle Eocene); GJV. Shell height 36 mm.

Figures 8–9. *Sulcoliva monilis* (Olsson, 1928); Parinas Sandstone (Early Eocene, Peru); PRI 3671. Shell height 17 mm.

Figures 10–12. *Pseudoliva crassa* (Gmelin, 1791); West Africa; CAS 063184. Shell height 25 mm.

Figures 13–15. *Luizia zebrina* (A Adams, 1855); Ilha de Luana, Angola; MNHN. Shell height 14.2 mm.

fasciolar ridge present or obsolete, bounded above by keel when present; anterior siphonal notch usually deep; umbilicus present or absent.

Stratigraphic and geographic distribution: Late Cretaceous (Campanian and Maastrichtian) of Europe, North Africa, southwestern Asia, and western South America; Early Paleocene to Late Eocene (Danian to Priabonian) of Europe, western and eastern North America, South America, North and sub-Saharan Africa; Early Paleocene of India; Late Eocene to Early Oligocene of Japan; ?Early Oligocene of Peru.

Discussion: The taxonomy, relationships, and generic nomenclature of Late Cretaceous and Paleogene pseudolivids remain matters of controversy and uncertainty. All species of this age are characterized by a pseudolivid groove that is situated at a relatively high position on the whorl, and by the absence of a parietal rib. In these important respects, they differ from the type genus *Pseudoliva*. In addition, Cretaceous and Paleogene pseudolivids usually show traces of axial sculpture, although it may be confined to apical whorls, especially in Eocene species. There is great variation in the degree of development of spiral and axial sculpture, in the presence or absence of a siphonal fasciole, in the height of the spire, and in the development of a subsutural channel. Many species have nodes or even spines at the shoulder or at the adapical ends of axial ribs, but in some species the upper part of the whorl is rounded and therefore unshouldered, and nodes are not developed.

Several authors have attempted to subdivide this group into genera, subgenera, or species groups. Among Paleocene and Eocene species with axial sculpture on the last whorl, Adegoke (1977) recognized but did not name a group of Paleocene species based on *Pseudoliva rogersi* Adegoke, 1977, from the Ewekoro Formation of Nigeria. It is characterized by reticulate sculpture, in which several rows of nodes form where strong spiral cords intersect axial riblets. Zinsmeister (1983) proposed the genus *Pegocomptus* for a very similar species, *Molopophorus howardi* Dickerson, 1914, from the Santa Susana Formation of southern California and the Sepultura Formation of Baja California Norte, Mexico. My examination of this Paleocene species shows that it lacks an umbilicus, whereas *Pseudoliva rogersi* has a wide, deep umbilicus (Adegoke, 1977).

Squires (1989) distinguished a second group of axially ribbed Paleocene and Eocene pseudolivids as his new genus *Calorebama*, for which he chose *Pseudoliva dilleri* Dickerson, 1914, as type. He characterized *Calorebama* as having an angulated, noded shoulder, shallow appressed suture, pseudolivid groove situated relatively high on the last whorl, and variably developed spiral sculpture that coarsens toward the base. Squires included in this group two species (*C. unicarinata* and *C. tuberculifera*) from the Paleocene of the Gulf Coastal Plain of the United States, as well as five subspecies of *C. dilleri* from the Eocene of western North America. Kase (1990) added his new species *C. cretacea* from the Late

Cretaceous (Campanian to Early Maastrichtian) of Japan. He included this species in *Calorebama* because of its resemblance to *C. dilleri inornata*, which like *C. cretacea* lacks shoulder nodes.

At least two of the characters of *Calorebama* mentioned by Squires (1989) are not generically diagnostic. All pseudolivids have spiral sculpture that coarsens toward the base, and a nodose shoulder, which occurs in many Late Cretaceous and later pseudolivids, is often variably expressed during ontogeny (Squires, 1989). A third character, the appressed suture, occurs in *Pegocomptus* as well as in several slender species of the *Pseudoliva koeneni* group (see below), in which the shoulder is not nodose.

Still another group that was recognized in this early welter of pseudolivids was *Popenoeum* (Squires et al., 1989). This genus, typified by *P. maritimus*, was characterized as having tabulate whorls, subsutural channel, axial ribs terminating as tubercles at the shoulder, a relatively thick columellar callus, and a well developed siphonal fasciole. Besides the type species and its subspecies *P. m. bajaensis*, Squires et al. (1989) included a wide variety of Cretaceous to Eocene species: *P. bocaserpentis*, *P. chavani* (Glibert, 1973, not Tessier, 1952; see below), *P. mutabilis* and its subspecies *woodsi*, *P. prima*, *P. robustum*, *P. scalina*, and *P. subcostata* (see Appendix 1). Kase (1990) subsequently assigned the Cretaceous species *P. praecursor* and *P. zitteli* to *Popenoeum*. Squires et al. (1989) explicitly excluded *P. mutabilis douvillei* from *Popenoeum*, apparently because of the extraordinary development of callus on the spire of that large Early Eocene form from Peru. My examination of the holotypes of *Pseudoliva mutabilis douvillei* and *P. m. woodsi* reveals broad similarities in shell shape and in the development of axial sculpture, and supports Olsson's (1928) suggestion that these two forms are closely related to each other and to *P. m. mutabilis*. *Pseudoliva mutabilis douvillei* has more prominent spines, which are directed abaxially, than does *P. m. woodsi*, whose spines are adapically directed.

Glibert (1973) defined an informal group of axially ribbed Paleocene pseudolivids as the group of *Pseudoliva koeneni*. Members of this European group are characterized by very small, slender shells with a linear rather than canaliculate suture. Most species, including *P. koeneni*, *P. elisae*, and *P. tenuicostata*, lack shoulder tubercles, but *P. curvicostata* does possess tubercles (see Glibert, 1973). Some of these species may be synonyms of each other, and some may prove to belong to *Fusopsis*, which is distinguished from other axially ribbed Paleogene pseudolivids by having a multispiral rather than paucispiral protoconch.

Many Late Cretaceous and Paleocene pseudolivids with axial sculpture on the last whorl were left out of these formal and informal groups. Some species combine features of several nominal groups. *Buccinum fissuratum* Deshayes, 1835, from the Late Paleocene (Thanetian) of the Paris Basin, for example, has a canaliculate suture like that of *Popenoeum*, but unlike *Popenoeum* it

has a rounded shoulder lacking nodes or tubercles. Spiral sculpture appears to be confined to the area below the pseudolivid groove, and is expressed at the edge of the outer lip as three crenulations. A siphonal fasciole is absent, as in *Calorebama dilleri kirbyi* and *Purpura pusilla*. *Buccinum laudunensis* Defrance, 1826, also from the Thanetian of the Paris Basin, is very similar *to B. fissuratum*, but its suture is appressed rather than canaliculate, and there is a low, distinct siphonal fasciole.

Moreover, the nominal groups differ in characters that vary intraspecifically and even during individual ontogeny. Wrigley (1941), for example, argued convincingly that a single Late Eocene species from northwestern Europe (Germany, Belgium, and England) is represented by a continuous series of forms between the types that have been called *Purpura nodulosa*, in which eight to ten axial ribs per whorl are enlarged by two rows of nodes, and *P. pusilla*, in which the axial riblets are smooth (see Beyrich, 1854). This species also varies in the expression of spiral sculpture below the pseudolivid groove (Wrigley, 1941). In many species, spiral sculpture covers most or all of the surface of the last whorl in ontogenetically young individuals, but it becomes restricted to the base in ontogenetically older ones. When describing *Pseudoliva libyca*, Quaas (1902) noted that young, strongly sculptured slender, high-spired individuals have a quite different appearance from larger individuals of the same species, in which the lateral profile of the relatively low spire is concave. Squires (1989) observed ontogenetic changes in spiral sculpture and in the presence of a subsutural swelling in species that he assigned to *Calorebama*.

It is therefore difficult to delineate well defined groups based on such characteristics as spire height, expression of spiral and axial sculpture, and presence of nodes among Cretaceous and Paleogene pseudolivids with axial sculpture. Although several lineages may be represented in this group, I prefer to treat the early, axially ribbed pseudolivids with a paucispiral protoconch as members of a single genus-level group.

In some Paleocene and Eocene pseudolivids, axial sculpture is confined to the spire whorls or is occasionally absent. Palmer (1937) used the taxon *Buccinorbis* Conrad, 1865, to encompass this group. Like Cossmann (1901) and Adegoke (1977), she regarded *Buccinorbis* as a subgenus or section of *Pseudoliva*. Fischer (1884) and Thiele (1929) synonymized *Buccinorbis* with *Pseudoliva*, whereas Squires (1989) and Vermeij and DeVries (1997) considered it to be a distinct genus. Conrad (1865:21) introduced *Buccinorbis* as a subgenus of *Sulcobuccinum* without diagnosis or comment. He included in it all eastern North American pseudolivids described up to 1865, including strongly sculptured species like *Pseudoliva tuberculifera* as well as the nearly smooth *Buccinum vetustum*. Cossmann (1901) designated *B. vetustum* Conrad, 1833, the last species Conrad (1865) listed as belonging to *Buccinorbis*, as type species.

The only character distinguishing *Buccinorbis* from most other early pseudolivids is the absence of axial sculpture on the last two teleoconch whorls. Species vary in the presence or absence of spiral sculpture on the upper part of the whorl, in spire height, in the presence or absence of an umbilicus, and in the development of columellar and parietal callus deposits. As pointed out by Olsson (1928), Palmer (1937), and Gardner (1945), these attributes vary during ontogeny, just as the expression of axial sculpture does. Ontogenetically young shells tend to be high-spired, to be axially sculptured, to have spiral cords or threads distributed over the whole surface of the whorl, to have an open umbilicus, and to have a relatively limited callus. The loss of axial sculpture likely occurred in several Paleocene lineages, and by itself does not constitute sufficient grounds for distinguishing *Buccinorbis* from other early pseudolivids with a paucispiral protoconch, high position of the pseudolivid groove on the whorl, and absence of a parietal rib. I therefore treat most of these species as belonging to a single genus.

The oldest available generic name for this group of pseudolivids is *Sulcobuccinum* d'Orbigny, 1850. This name has been overlooked by most authors, perhaps in part because Fischer (1884), Cossmann (1901), Thiele (1929), and Wenz (1938–44) synonymized it with *Pseudoliva* without discussion. D'Orbigny (1850:303) compared his genus with *Buccinanops* d'Orbigny, 1841 (Nassariidae, Dorsaninae; see Allmon, 1990), and listed three species as belonging to it: *Buccinum fissuratum* Deshayes, *B. tiara* Deshayes, and *B. semicostatum* Deshayes. Among these, *B. semicostatum* is a junior synonym of *Buccinum laudunense* Defrance (see Glibert, 1960; Villatte, 1970), and *B. tiara* is a junior synonym of *Struthiolaria prima* Defrance (Villatte, 1970). Coquand (1862) added a fourth species, *S. michelini*; and Conrad (1865) introduced *Buccinorbis* as a subgenus of *Sulcobuccinum*. Neither d'Orbigny (1850) nor any subsequent author designated a type species of *Sulcobuccinum*. Because *Buccinum fissuratum* Deshayes, 1835, was the first species listed by d'Orbigny (1850), I here designate it as the type species of *Sulcobuccinum* d'Orbigny, 1850.

Several genera have in common with *Sulcobuccinum* the presence of axial sculpture on the last whorl. These include *Benthobia*, *Fusopsis*, *Fusulculus*, *Hubachia*, *Luizia*, and *Sulcoliva*. As discussed further under *Fusopsis*, *Sulcobuccinum* differs from that Paleocene group mainly by having a paucispiral protoconch rather than a multispiral one. Most species of *Sulcobuccinum* are not basally constricted, in contrast with *Fusopsis*. The study of protoconchs may reveal a diversity of types among species currently assigned to *Sulcobuccinum*. In addition, further work may show that *Fusopsis* is conchologically indistinguishable from *Benthobia*. *Sulcobuccinum* differs from *Fusulculus* by the presence of a posterior notch on the outer lip and by lacking the basal constriction of the last whorl. It differs from *Luizia* by the absence of riblets on the inner side of the outer lip, and from *Sulcoliva* by having a deep pseudolivid groove and by not having axial ribs confined to a narrow peripheral band

In reviewing the species here assigned to *Sulcobuc-*

cinum, I have uncovered a case of homonymy. Glibert (1973) named *Pseudoliva chavani* from the Calcaire de Mons (Danian, Early Paleocene) of Belgium. Unfortunately, this name is preoccupied by *Pseudoliva (Buccinorbis) chavani* Tessier, 1952, from the Maringot de Balling (Paleocene) of Senegal. I therefore rename Glibert's species *Sulcobuccinum multinodulosum*, new name, to emphasize the large number (seventeen to nineteen) of axial riblets forming nodules below the suture.

Nearly all Late Cretaceous species of *Sulcobuccinum* are known from the Old World (see Appendix 1). These include *S. aaronsohni* and *S. moabiticum* from the Senonian of Palestine, *S. cretaceum* from the Campanian to Early Maastrichtian of Japan, *S. praecursor* and *S. zitteli* from the Senonian of Hungary, *S. sofegginense*, *S. libycum*, and *S. subcostatum paucicostatum* from the Maastrichtian of North Africa, and *S. ambiguum* from the type Maastrichtian in the Netherlands and perhaps the Maastrichtian of Tunisia (for species accounts see Quaas, 1902; Pervinquière, 1912; Blanckenhorn, 1927; Rossi Ronchetti, 1959; Kase, 1990). Although I have not examined these Late Cretaceous species, the differences among them seem slight, and there may be many fewer species than there are available names. The only New World members of *Sulcobuccinum* from the Late Cretaceous are Olsson's (1934) *Pseudoliva* sp. from the Maastrichtian of northern Peru, represented by a single, poorly preserved specimen, and Muniz's (1993) *Pseudoliva bellecompta*, a cancellate species from the Gramame Formation (Campanian) of northeastern Brazil. Oddly enough, the genus is unknown from the Cretaceous of sub-Saharan Africa, Madagascar, and North America. All Cretaceous species have a relatively high spire, the last whorl comprising 80% or less of the total shell height, and all have well developed axial sculpture on the spire whorls as well as the last whorl.

During the Paleocene, the genus *Sulcobuccinum* was widely distributed in warm seas, with an apparent center of diversity around the North Atlantic (see Appendix 1). Species such as *S. koeneni* from Denmark, *S. multinodulosum* from Belgium, *S. rosenkrantzi* from Austria, and *S. minutissimum* from Morocco are high-spired, axially ribbed, very small forms not exceeding 7 mm in shell height. By contrast, the European *S. prima* reaches a height of 65 mm and has a spinose shoulder.

Several Old World Paleocene species show trends toward a reduction in axial sculpture. One such group of species is represented in the Ewekoro Formation of Nigeria by *S. adelekei*, *S. f. funkeanum*, and *S. f. ornatum*. Adegoke (1977) characterized this group as high-spired, spirally sculptured, and having a narrow elevated callus and a rounded rather than shouldered upper part of the whorl. These Paleocene species are small (maximum height of *S. adelekei*, USNM 174853, 12.0 mm). In the Ameki Formation (Middle Eocene) of Nigeria, this group is represented by the larger *S. kitsoni* (maximum height 47.1 mm). This is a high-spired species (last whorl comprising 70 to 80% of total shell height) with a pari-

etal swelling at the adapical end of the inner lip. Related Eocene species include *S. thielei* and *S. leutweini* from Namibia and *S. eschi* from Cameroon. Böhm (1926) described *S. thielei* as having an umbilicus, a moderately high spire (last whorl comprising 84% of total shell height), relatively large size (maximum height 50 mm), and spiral sculpture persisting on the last whorl only near the suture and below the pseudolivid groove. Besides being slightly lower-spired, *S. thielei* appears to be very similar to *S. kitsoni* and probably represents the same species, which would then take the name *S. kitsoni* (Newton, 1922).

A second group in which axial sculpture has become reduced is represented in the Ewekoro Formation of Nigeria by *S. guineense*. This species has a minute, very low spire, a well developed callus extending on the spire, a distinct siphonal fasciole, and axial sculpture consisting of fifteen to sixteen ribs on spire whorls but absent on the last two whorls. The slightly older *S. chavani* from the Danian (Early Paleocene) of Senegal is very similar, but its axial sculpture extends to the last whorl (see Tessier, 1952). *Sulcobuccinum guineense* and the *S. adelekei* group represent two apparently independent transitions from typical *Sulcobuccinum* in which axial sculpture continues to adulthood, to the *Buccinorbis* phenotype, in which the last one or two whorls are free of axial sculpture.

Eocene representatives of *Sulcobuccinum* were highly diverse in form and size. Strongly tuberculate or spiny species include *S. mutabile* and its subspecies *S. m. woodsi* and *S. m. douvillei* from the Early and Middle Eocene of Peru (see Olsson, 1928; Squires *et al.*, 1989) and *S. michelini* from the Middle Eocene (Suessonian) of North Africa (for discussion see Salvan, 1954). Small, slender, axially ribbed species include *S. bussoni* from the Early Eocene of southern Tunisia (see Albanesi & Busson, 1974) and *S. pusillum* from the Lattorfian (latest Eocene) of northwestern Europe. The name *Purpura pusilla* Beyrich, 1854 (pp. 143–144) has page priority over the synonymous *P. nodulosa* Beyrich, 1854 (p. 144), and must therefore stand as the valid name for this small, sculpturally variable species. Relatively low-spired species with a tuberculate shoulder and variably developed axial sculpture on the last whorl include *S. schweinfurthi* from Cameroon (see Oppenheim, 1904) and the forms that Squires (1989) subsumed under the name *Calorebama dilleri* from the Early to Late Eocene (Ypresian to Priabonian) of western North America. These western North American forms overlap greatly in form, sculpture, and stratigraphic distribution (Squires, 1989), and may well represent a single, variable, stratigraphically long-lasting, widely distributed species whose earliest valid name is *Sulcobuccinum lineatum* (Gabb, 1864). A large (perhaps 50 mm high), axially ribbed species without a tuberculate shoulder from the latest Eocene (Lattorfian) of Helmstedt, Germany, was described as *Pseudoliva rudis* on the basis of one poor specimen by von Koenen (1889). The distinctive Middle Eocene *S. coronaria* from Peru is characterized by large size

(height 50 mm), a high spire, and a nodose, sharply shouldered last whorl (see Olsson, 1930). Several species groups of *Sulcobuccinum* lack axial sculpture on the last one or more teleoconch whorls, and were therefore previously assigned to the genus, subgenus, or section *Buccinorbis*. Besides *S. kitsoni*, which I discussed above, this group includes many species in North and South America, Europe, and one in Japan.

The Old World group of slender species of the *Buccinorbis* phenotype, typified by *S. adelekei* and *S. kitsoni* (see above), is represented in the early Eocene of the Gulf Coastal Plain of the United States by *S. ostrarupis* from Alabama and by the Texan subspecies *S. o. pauper.* These forms have a high spire (last whorl comprising 67% to 76% of total shell height), a narrow aperture, and an obsolete pseudolivid groove. The last whorl is rounded above and evenly tapered below, and lacks an umbilicus and siphonal fasciole. It is possible that some of these characters are those of juvenile specimens, but another possibility is that the *S. ostrarupis* group is plesiomorphic with respect to features of the spire and base.

The species group of *S. vetustum* (type species of *Buccinorbis*) occurs on the Gulf Coastal Plain of the southeastern United States (see Palmer, 1937; Dockery, 1980). *Sulcobuccinum vetustum,* from the Gosport Sand (Middle Eocene) of Alabama, has an appressed suture, closed umbilicus, low spire (last whorl comprising more than 90% of shell height), and obsolete spiral cords on the upper part of the last whorl. Grooves between five cords below the pseudolivid groove end in sharp crenulations at the outer lip. In my material from Little Stave Creek, Alabama, most individuals have a relatively restricted callus, but one large individual (height 34.1 mm) has the spire nearly obliterated by a massive callus deposit. *Sulcobuccinum carinatum* and *S. perspectivum* are related species with an open umbilicus. Although Palmer (1937) regarded them as forms of *vetustum,* my examination of this group reveals subtle but consistent differences. *Sulcobuccinum carinatum* from the Stone City and Cook Mountain Formations of Texas (Middle Eocene) and *S. perspectivum* from the Moodys Branch Formation of Mississippi (Late Eocene) are somewhat higher-spired (last whorl comprising 81 to 83% of shell height) than is *S. vetustum.* The last whorl of *S. carinatum* is somewhat less slender (whorl diameter-to-whorl height ratio 0.93) than that of *S. perspectivum* (ratio 0.86), but the shell of *S. carinatum* has a somewhat more slender appearance because the widest point of the last whorl lies at a relatively lower position and because the shoulder is less wide than the periphery in *S. carinatum.* Other species in this group include *S. linosum, S. nanum,* and *S. santander* from the Gulf Coastal Plain, and the nonumbilicate *S. obtusum* from France. Dockery (1980) speculates that the thick callus deposits of *S. santander* from the Bashi Marl Member of the Hatchetigbee Formation (early Eocene) of Mississippi indicate a gravitationally stable shell in a wave-swept, shallow-water environment. Similar callus deposits are developed in co-

occurring species of *Ancillopsis* and in several volutid gastropods.

Vermeij and DeVries (1997) reviewed a group of large (height up to 50 mm), nonumbilicate, smooth species from Peru, in which the outer lip is adapically extended beyond the tip of the spire in mature shells. This group, which may have extended into the Early Oligocene (T. J. DeVries, personal communication), includes *P. retusum* and its subspecies *S. r. samanicum* and *S. r. mancorense,* as well as *S. tientoense* and a form comparable to *S. retusum* from Colombia and Curaçao (see also Clark & Durham, 1946; Jung, 1974).

One species of the smooth *Buccinorbis* phenotype is known from Japan. Although originally described as a species of *Orthaulax* by Nagao (1924), the affinities of *S. japonicum* with *Pseudoliva* were recognized by Nagao (1928) by virtue of the presence of a pseudolivid groove. Honda (1991, 1994) records this species, in which axial sculpture is absent and spiral sculpture is confined to the zone below the pseudolivid groove, from Late Eocene (Takashiman and Okinoshiman) and Early Oligocene (Mazean and Funazuan) deposits.

Genus *Hubachia* Etayo Serna, 1979
(Figure 4)

Type species: *Hubachia ramirolobae* Etayo Serna, 1979, by original designation.

Diagnosis: Shell medium-sized, maximum height about 30 mm, ovate; protoconch unknown; spire moderately low to very low, last whorl comprising 81 to 100% of total shell height; last whorl marked by low, sharply angulate shoulder, immediately below which is a deep spiral groove; between upper groove and pseudolivid groove, last whorl evenly rounded; base of last whorl not constricted; spiral sculpture consisting of fine spiral threads on spire whorls, and of eight weak cords below pseudolivid groove on last whorl; axial sculpture confined to spire whorls, consisting of about 15 irregular, rounded, low ribs; pseudolivid groove situated high on last whorl, just below its middle; outer lip unknown; aperture broadly ovate, its height-to-breadth ratio approximately 2.0; columellar and parietal callus thick, well developed ventrally, but not extending onto spire; umbilicus absent.

Stratigraphic and geographic distribution: Paleocene, Colombia.

Discussion: Etayo Serna (1979:37) introduced *Hubachia* as a monotypic genus of the family Olividae from the Paleocene of Colombia. He noted that *Hubachia* differs from the olivid genus *Olivancillaria* d'Orbigny, 1839, by having axial sculpture on the spire whorls and by having basal cords on the basal half of the last whorl. Etayo Serna (1979) also noted the presence of a pseudolivid groove, and remarked on the similarity of *Hubachia* to *Pseudoliva,* from which it differs by the presence of axial sculpture on the spire whorls.

Poor preservation of the available specimens precludes detailed comparison with other genera, and forces me to consider the assignment and status of *Hubachia* as provisional. The very deep spiral groove immediately below the sharply angled shoulder distinguishes *Hubachia* from other pseudolivid genera. *Hubachia* has an unusually broad aperture and low spire, and has a rounded periphery well below the shoulder. It superficially resembles some species of *Sulcobuccinum* in having axial sculpture confined to the spire whorls, but diverges from species of *Sulcobuccinum* in which axial sculpture is absent on the last whorl by the sharp shoulder and accompanying groove.

Hubachia differs from *Sulcobuccinum* by having axial sculpture confined to the early teleoconch whorls, by the exceptionally low spire, and by the presence of a very deep groove just below the sharply angulate shoulder. The periphery of the last whorl is evenly rounded in *Hubachia*. The aperture of *Hubachia* is relatively very broad compared to that in species of *Sulcobuccinum* and *Buccinorbis*. *Hubachia* differs further from *Buccinorbis* by the character of the shoulder and its accompanying groove.

Genus *Benthobia* Dall, 1889

Type species: *Benthobia tryonii* Dall, 1889, by original designation.

Synonym:
Nux Barnard, 1960 [Type species: *Nux alabaster* Barnard, 1960 (= *Benthobia triennia* Dall, 1889)].

Diagnosis: Shell small, maximum height 13 mm, thin; protoconch multispiral; spire moderately low, last whorl comprising 75 to 77% of total shell height; last whorl inflated, evenly rounded above, not constricted basally; spiral sculpture obsolete; axial sculpture consisting of numerous very fine, short riblets confined to subsutural ramp and shoulder; pseudolivid groove very shallow, situated just below middle of last whorl; outer lip with obsolete labral tooth; inner side of outer lip smooth; posterior notch absent; aperture ovate, its height-to-breadth ratio 2.0 to 2.3; columellar and parietal callus thin, of very limited extent; parietal ridge absent; siphonal fasciolar ridge absent; anterior siphonal notch obsolete; umbilicus absent.

Stratigraphic and geographic distribution: Recent, bathyal and abyssal eastern and western Atlantic Ocean from 38°N to 33°S; southwestern Indian Ocean; off New Zealand; 800 to 4380 m.

Discussion: Dall (1889:131) originally placed his new genus *Benthobia* in the family Cancellariidae because of its superficial resemblance to *Admete* Kroyer *in* Moller, 1842; but he expressed doubts about this assignment in view of the absence of anatomical information. The absence of columellar folds also implied that *Benthobia* was unlikely to belong to the Cancellariidae. Bouchet and Warén (1985) figured the radula of *Benthobia* and

transferred the genus to the olivid subfamily Pseudolivinae. Kantor's (1991) anatomical work subsequently provided further support for this reassignment.

As presently understood, *Benthobia* is a monotypic genus of Recent bathyal and abyssal gastropods. Anatomically, *Benthobia* is plesiomorphic in having the radular sac situated at the base of the proboscis and by retaining the connection between the radular retractor muscle and columellar muscle (Kantor, 1991).

Among living Pseudolividae, *Benthobia* is unique in having a multi-spiral protoconch, which Bouchet and Warén (1985) link to planktotrophic development. This character is shared with the Paleocene genus *Fusopsis*. *Benthobia* and *Fusopsis* have many features in common, and further work may indicate that *Fusopsis* represents an early appearance of *Benthobia*. Both genera have axial sculpture confined to the upper part of the whorl. *Fusopsis* differs from *Benthobia* mainly by having a slightly constricted base.

Another similar genus is *Fusulculus*, which like *Benthobia* has a very shallow anterior siphonal notch. Both genera lack a posterior notch and parietal rib. *Fusulculus* differs from *Benthobia* by being basally constricted. The spire of *Fusulculus* is higher, and spiral sculpture is well developed on the base. *Fusulculus* bears a small but distinct labral tooth as well as several crenulations below the tooth on the outer lip, whereas in *Benthobia* the tooth is obsolete and crenulations are absent.

The genus *Zemira* resembles *Benthobia* in lacking a fasciole and basal constriction and in having a very shallow anterior siphonal notch. It differs by having well developed spiral sculpture, by possessing a distinct labral tooth, and (in the type species) by lacking any trace of axial sculpture.

Genus *Fusopsis* Ravn, 1939.

Type species: *Pseudoliva (Fusopsis) canalifera* Ravn, 1939.

Diagnosis: Shell very small, maximum height 3.5 mm, relatively high-spired; last whorl comprising 70% of shell height; protoconch multispiral; shell fusiform, constricted at base of last whorl; teleoconch whorls convex, separated by deep, canaliculate suture; spiral sculpture consisting of 10 threads on last whorl; axial sculpture consisting of 12 riblets on upper part of last whorl; pseudolivid groove situated just below middle of last whorl, forming small labral tooth at edge of outer lip; umbilicus lacking (surmised from description of type species by Ravn, 1939).

Stratigraphic and geographic distribution: Paleocene of Denmark.

Discussion: Ravn (1939:76) introduced *Fusopsis* as a subgenus of *Pseudoliva* in the course of describing *Pseudoliva canalifera* from the Paleocene of Copenhagen, Denmark. Although he did not provide a diagnosis for the subgenus, he made it clear that *Fusopsis* differs from

Pseudoliva s.s. by having a multispiral rather than a pau-cispiral protoconch. Ravn (1939) was apparently unaware of the genus *Benthobia,* which like *Fusopsis* has a multispiral protoconch, but which was then classified in the Cancellariidae.

Without the protoconch, *Fusopsis* would be indistinguishable from other relatively high-spired species of small, Paleocene pseudolivids that I assign here to the genus *Sulcobuccinum.* In fact, Ravn (1939) pointed out that *Pseudoliva koeneni* Ravn, 1939, which co-occurs with *Fusopsis canalifera,* is transitional to more typical "*Pseudoliva*" (= *Sulcobuccinum* as used in this paper). *Fusopsis canalifera* differs from most species of *Sulco-buccinum* by being basally slightly constricted. It is possible that several species here tentatively assigned to *Sul-cobuccinum* will prove to belong to *Fusopsis,* which, as discussed under *Benthobia,* may itself fall as a junior synonym of *Benthobia.*

Genus *Sulcoliva,* new genus
(Figures 8–9)

Type species: *Pseudoliva monilis* Olsson, 1928.

Diagnosis: Shell moderately small, maximum height 27.4 mm, narrowly ovate to biconic; protoconch unknown; spire high, last whorl comprising 59 to 75% of total shell height; sutures appressed; rounded above, slightly or not constricted basally; spiral sculpture consisting of 14 to 16 weak threads below pseudolivid groove on last whorl; axial sculpture consisting of 20 to 25 low, weak beads on periphery of last whorl, not visible on spire whorls; pseudolivid groove at high position on last whorl, expressed as stepwise basal narrowing rather than as a groove; outer lip with small labral tooth; posterior notch weak; aperture elongate-ovate, its height-to-breadth ratio 2.4 to 3.0; columellar and parietal callus of very limited extent; siphonal fasciolar ridge low, rounded; anterior siphonal notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Early to Late Eocene, Peru.

Included species: *Pseudoliva monilis* Olsson, 1928; *Pseudoliva modesta* Olsson, 1928.

Discussion: I propose the new genus *Sulcoliva* for two unusual pseudolivids from the Eocene of Peru described by Olsson (1928). *Sulcoliva* resembles *Sulcobuc-cinum,* but is distinguished by the high spire and by the presence of a peripheral band of fine beads. In *Sulco-buccinum,* axial sculpture, when present, normally extends from the suture to a point above the pseudolivid groove; whereas in *Sulcoliva* the axial riblets are confined to the periphery and cannot be seen on the spire whorls. Moreover, whereas the pseudolivid groove in *Sulcobuccinum* is deep, that of *Sulcoliva* has an adapical but not an abapical edge. The groove is therefore more like a step, a sudden, very slight abapical narrowing of the whorl at or just below mid-whorl height. *Sulcoliva* also resembles the Recent genus *Naudoliva.* Both gen-

era have a high-spired shell with an ill-defined pseudolivid groove and a distinct labral tooth. *Naudoliva* differs from *Sulcoliva* by lacking axial sculpture and by the absence of a posterior notch.

The genus *Sulcoliva* contains two species from the Eocene of northern Peru. These are *S. monilis,* the type species, from the Parinas Sandstone (Early Eocene), and the higher-spired, somewhat larger *S. modesta* from Olsson's (1930) Talara Formation (Late Eocene, Bartonian).

Genus *Naudoliva* Kilburn, 1989

Type species: *Naudoliva caitlinae* Kilburn, 1989, by original designation.

Diagnosis: Shell thin, ovate, of medium size, maximum height 29 mm; protoconch paucispiral; spire relatively high, last whorl comprising 64% to 69% of total shell height; suture appressed or impressed; last whorl with concave subsutural ramp, a rounded or weakly angulated shoulder, and an unconstricted base; spiral sculpture consisting of very fine threads on spire whorls and on base of last whorl; axial sculpture absent (*N. cait-linae*) or consisting of short, rounded ribs at shoulder above periphery (*N. vorsteri*); outer lip planar, with long labral tooth; inner side of outer lip smooth; posterior notch absent; aperture elongate-ovate, its height-to-breadth ratio about 2.7; columella and parietal callus thin, not extensive; columella without fold at base; parietal rib absent; siphonal fasciole low, rounded, sculptured with very fine spiral threads; umbilical slit very narrow or absent; anterior notch deep; periostracum absent.

Stratigraphic and geographic distribution: Late Miocene, Trinidad; Recent, Indian Ocean coast of South Africa.

Discussion: Kilburn (1989) proposed *Naudoliva* to accommodate *N. caitlinae,* a distinctive pseudolivid characterized by a high spire, small umbilical slit, and very fine spiral but no axial sculpture. The shell has an unusually long labral tooth, situated at the end of shallow, broad pseudolivid groove on the lower third of the last whorl. There is no periostracum. Kilburn noted that the radula has a unicuspidate lateral plate, as in *Benthobia* (Kantor, 1991), and that the head tentacles are bilobed, as in *Luizia zebrina* (Kantor, 1991). *Pseudoliva,* by contrast, has a bicuspidate lateral plate and single head tentacle. The latter character also occurs in *Zemira* (see Ponder & Darragh, 1975; Kantor, 1991). The absence of a posterior notch on the outer lip is a character that *Naudoliva* has in common with *Benthobia* and *Fusul-culus. Naudoliva* differs from these genera by having a long labral tooth, deep anterior siphonal notch, and a low but distinct siphonal fasciole. It differs from *Luizia* by having a smooth instead of lirate inner side of the outer lip, and by lacking a posterior notch.

The type species, *N. caitlinae,* is from Transkei, South Africa. Its shell is very slightly constricted at the base,

and lacks axial sculpture. *Naudoliva vorsteri*, recently described by Lussi (1995) from Algoa Bay, differs from *N. caitlinae* by lacking the basal constriction and by having about ten short axial ribs at the shoulder. These ribs do not extend up to the suture or down to the gently rounded periphery, and become obsolete near the outer lip. The absence of the periostracum characterizes both species, and readily distinguishes this unusual genus from other South Africa pseudolivid (see also Lussi, 1995).

Mansfield (1925) described *Pseudoliva guppyi* on the basis of a single, exquisitely preserved specimen from the Springvale Formation (Late Miocene) of Trinidad. My examination of the holotype reveals that the shell is moderately high-spired, the last whorl comprising 73% of total shell height. The last whorl is not constricted at the base; it is sculptured by very faint spiral threads, and below the pseudolivid groove by more prominent spiral cords. The low shoulder is marked by sixteen short, weak axial ribs. The shallow pseudolivid groove is situated just below the middle of the last whorl, and ends in a relatively long, sharp labral tooth. The inner side of the outer lip is smooth. The aperture is ovate, its height-to-breadth ratio being about 2.3. A posterior notch, parietal rib, siphonal fasciole, and umbilicus are lacking. The anterior siphonal notch is deep.

I assign Mansfield's species provisionally *Naudoliva*. It is very similar in form and sculpture to *N. vorsteri*, from which it differs in having a larger number of axial ribs (sixteen versus ten), a broader aperture (apertural height-to-breadth ratio 2.3 instead of 2.7), and a smaller shell (10.4 versus 29.4 mm). The only significant feature of *Pseudoliva guppyi* that is inconsistent with assignment to *Naudoliva* is the absence of a siphonal fasciole, which is low and weak in *Naudoliva*. In the absence of a fasciole, *P. guppyi* resembles *Fusulculus*, with which it additionally has in common the numerous short axial riblets and the absence of a posterior notch. *Pseudoliva guppyi* differs from *Fusulculus*, however, in not being constricted at the base, in having a long labral tooth, a much deeper siphonal notch, a relatively broader aperture, and a shorter spire. It is possible that the absence of a siphonal fasciole in the Miocene fossil as well as in species of *Fusulculus*, *Benthobia*, and *Zemira* is a juvenile or neotenic feature. For now, it seem best to assign *Pseudoliva guppyi* to *Naudoliva*, despite the great geographic distance between Trinidad and the South African localities where the other two species of *Naudoliva* occur.

Naudoliva guppyi is only one of two pseudolivids known from the tropical western Atlantic Neogene, the other being *Macron constrictus* from the early Miocene of Venezuela. As noted by Mansfield (1925), there is no living or fossil tropical American species that is even remotely similar to this unusual late Miocene species from Trinidad.

Genus *Luizia* Douvillé, 1933

Type species: *Buccinum* (*Luizia*) *costae* Douvillé, 1933, by original designation.

Diagnosis: Shell small, maximum height 22 mm; ovate; protoconch paucispiral; sutures appressed; spire moderately high, last whorl comprising 77 to 83% of total shell height; last whorl shouldered above, not constricted basally; spiral sculpture consisting of very fine threads over whole shell surface; axial sculpture consisting of 14 to 17 riblets on upper part of whorl, forming nodes at shoulder; pseudolivid groove situated high on last whorl, about one-third the distance from the anterior end of the shell; outer lip planar, with small, distinct labral tooth; inner side of outer lip with 11 to 12 lirae; posterior notch shallow; aperture narrowly elongate, its height-to-breadth ratio 3.3; columellar and parietal callus thin, of very small extent; parietal rib absent; siphonal fasciole bounded posteriorly by low keel; anterior notch deep; umbilicus absent.

Stratigraphie and geographic distribution: Early? Miocene to Recent, Angola.

Discussion: Douvillé (1934) proposed *Luizia* as a subgenus of *Buccinum* for a small gastropod from the Miocene (probably Burdigalian, Early Miocene) of Angola. Although he noted the presence of a pseudolivid-like groove on the lower part of the last whorl, Douvillé (1934) assigned *Luizia* to *Buccinum* because of its weak axial riblets and spiral threads. In the Recent fauna, *Luizia* is represented by *Pseudoliva zebrina* A. Adams, 1855, from Angola (Figure 13–15). This species has a small shell (maximum height 19.2 mm) with a relatively high spire (last whorl comprising 77 to 83% of total shell height), 14 to 17 weak axial riblets forming nodes at the shoulder crossed by very weak threads. The inner side of the outer lip bears 11 to 12 weak lirae.

The genus *Luizia* closely resembles *Naudoliva*, *Fusulculus*, and slender species of *Sulcobuccinum*. It differs from all these by having the inner side of the outer lip lirate (sculptured by small riblets) instead of smooth. *Luizia* differs from *Fusulculus* and *Naudoliva* by having a weak posterior notch, and from *Fusulculus* by the presence of a siphonal fasciole and by lacking a basal constriction on the last whorl.

Genus *Fusulculus* Bouchet & Vermeij, 1998

Type species: *Fusulculus crenatus* Bouchet & Vermeij, 1998, by original designation.

Diagnosis: Shell relatively small, maximum height 18.4 mm, fusiform; protoconch paucispiral; sutures appressed; spire relatively high, last whorl comprising 61 to 67% of total shell height; last whorl with concave subsutural ramp, a rounded shoulder, and basal constriction; spiral sculpture consisting of up to 15 weak cords between shoulder and base, sometimes obsolete; axial sculpture consisting of 14 to 16 riblets extending from the suture to a point just below the shoulder; pseudolivid groove at lip convex ventrally, with very weak labral tooth and five weak basal crenulations; inner side of outer lip smooth; posterior notch obsolete; aperture narrowly

ovate, its height-to-breadth ratio 2.6 to 3.2; columellar and parietal callus thin, of very limited extent; parietal rib absent; siphonal fasciole and umbilicus absent; anterior notch shallow.

Stratigraphic and geographic distribution: Recent, bathyal southwestern Pacific from Coral Sea and New Caledonia to north of New Zealand.

Discussion: The genus *Fusulculus* resembles *Benthobia* and *Zemira* in having a very shallow anterior siphonal notch, a limited extent of callus, a high position of the pseudolivid groove on the last whorl, and in lacking a parietal rib at the adapical end of the inner lip. *Fusulculus* differs from these genera by being constricted at the base, and from the type species of *Zemira* by having well developed axial sculpture. *Naudoliva* and *Fusulculus* have in common the absence of a posterior notch on the outer lip, but *Fusulculus* is distinctly constricted at the base, whereas *Naudoliva* has little or no basal constriction. Moreover, *Naudoliva* has a low, rounded siphonal fasciole and a deep siphonal notch, features lacking in *Fusulculus*.

Bouchet and Vermeij (1997) describe two species, *F. crenatus* and *F. albus*, from bathyal waters in the southwestern Pacific. These species are the only pseudolivids living in the tropical Indo-West Pacific.

Genus *Zemira* H. & A. Adams, 1853

Type species: *Eburna australis* G. B. Sowerby, 1833, by monotypy.

Synonym:
Eburnopsis Tate, 1889 (type species: *Eburnopsis aulacoessa* Tate, 1889, = *Zemira australis*, *fide* Ponder & Darragh, 1975)

Diagnosis: Shell relatively small, maximum height 21 mm, ovate; protoconch paucispiral; spire moderately high, last whorl comprising 66 to 68% of total shell height; sutures deeply channeled; last whorl rounded above, not constricted basally; spiral sculpture consisting of as many as 25 weak flattened cords between suture and base of last whorl, the six to seven cords below pseudolivid groove widest; axial sculpture absent; pseudolivid groove situated high on last whorl, just below its midpoint; outer lip with distinct labral tooth and basal crenulations; inner side of outer lip smooth; posterior notch present; aperture ovate, its height-to-breadth ratio 1.9 to 2.2; columellar and parietal callus thin, of very limited extent; parietal rib absent; siphonal fasciole absent; anterior siphonal notch obsolete; umbilicus usually absent.

Stratigraphic and geographic distribution: Late Eocene to Recent, Australia

Discussion: Ponder and Darragh (1975) have fully reviewed the living and fossil species of *Zemira* and provided anatomical details for the two living species, *Z. australis* (northern New South Wales to Tasmania) and *Z. bodalla* (southern Queensland). H. & A. Adams

(1853) proposed *Zemira* as a member of the muricid subfamily Purpurinae because of characters of the radula. Fischer (1884) regarded *Zemira* as a section of *Macron* in the Buccinidae. Cossmann (1901) assigned it to the buccinid subfamily Latrunculinae (= Babyloniinae). Ponder and Darragh's (1975) anatomical work revealed similarities to *Pseudoliva*, and suggested that the radular similarities with Purpurinae (= Ocenebrinae and Rapaninae) result from inheritance of plesiomorphic character states (see also Kantor, 1991).

Zemira resembles *Fusulculus* in its relatively high spire, position of the pseudolivid groove, lack of a siphonal fasciole, and obsolete anterior notch. It differs from *Fusulculus* by lacking the basal constriction, by having a deeply channeled suture, and by lacking axial sculpture in most species. The labral tooth is distinct in *Zemira* but obsolete in *Fusulculus*. *Zemira* differs from *Benthobia* by having a higher spire, a much less inflated last whorl, well-developed spiral sculpture, a posterior notch, and a labral tooth. Axial sculpture, which is present as short riblets on the upper part of the whorl in *Benthobia*, is lacking in *Zemira* .

The type species of *Zemira* , *Z. australis*, is interpreted by Ponder and Darragh (1975) as a long-ranging, variable species. It includes *Eburnopsis aulacoessa* Tate, 1889 and *Zemira praecursoria* Tate, 1888, which are heavily corded and smooth forms respectively from the Balcombian (middle Miocene) of Victoria. The spire of *Z. australis* is generally higher than in other species of the genus. Axial sculpture is absent in *Z. australis* and in its presumed progenitor, *Z. australis antecursoria*, from the Longfordian and Batesfordian (early Miocene) of Victoria; but it is present in *Z. tessellata*, the Late Oligocene ancestor of the *Z. australis* lineage from the Jan Juc Formation of Victoria (Ponder & Darragh, 1975). An umbilicus is absent in *Z. a. australis*, but is variably developed in the other species assigned by Ponder and Darragh (1975) to *Zemira* . The earliest representative of *Zemira* recognized by Ponder and Darragh (1975) is an undescribed species from the Glen Aire Clay (Late Eocene) of Victoria. This species lacks axial sculpture and has a wide umbilicus.

Genus *Testallium* Vermeij & DeVries, 1997.

Type species: *Gastridium cepa* Sowerby, 1846, by original designation.

Synonyms:
Gastridium Sowerby, 1846 (type species: *Gastridium cepa* Sowerby, 1846), *non* Modeer, 1793, *nec* Sowerby, 1842.

Diagnosis: Shell large, maximum height 57 mm, broadly fusiform; protoconch unknown; last whorl rounded or shouldered above, constricted basally; spiral sculpture variably expressed, consisting of cords that are strongest below pseudolivid groove; axial sculpture usually absent, or when present is confined to spire whorls (*T. voluta*); pseudolivid groove at low position on last whorl; outer lip planar, with distinct labral tooth and

about five basal crenulations; posterior notch present; aperture ovate, its height-to-breadth ratio 1.9 to 2.4; columellar and parietal callus of limited extent but may be thick; parietal rib present; siphonal fasciole strong, bounded above by prominent keel; anterior notch deep; umbilicus present or absent.

Stratigraphic and geographic distribution: Early Miocene to Late Pliocene, temperate western South America.

Discussion: Vermeij and DeVries (1997) have given a full account of the synonymy and composition of the genus *Testallium* from the Miocene and Pliocene of temperate western South America. The name *Gastridium* Sowerby, 1846, which has been used previously for these species (Sowerby, 1846; Philippi, 1887; Herm, 1969), is preoccupied by *Gastridium* Modeer, 1793 (Conidae) and *Gastridium* Sowerby, 1842 (a synonym of *Pseudoliva*). Von Ihering (1907) referred species of Sowerby's (1846) *Gastridium* to *Austrocominella* von Ihering, 1907, which he proposed as a subgenus of *Cominella* Gray, 1850. Allmon (1990) and Beu & Maxwell (1990) have pointed out that *Cominella (Austrocominella) fuegensis* von Ihering, 1907, the type species of *Austrocominella* from the Rio Turbio and Loreto Formations (Early? Miocene of Tierra del Fuego), is closely related to or belongs in the same genus as does *Zelandiella subnodosa* (Hutton, 1877), the type species of *Zelandiella* Finlay, 1926, from the Altonian (Early Miocene) of New Zealand. Von Ihering (1907) mistakenly believed that the South American species of *Gastridium* Sowerby, 1846, lack a pseudolivid groove. The inclusion of these species in *Austrocominella,* which indeed does lack a pseudolivid groove, was therefore unwarranted. Species of *Gastridium* have also occasionally been confused with members of the ocenebrine muricid genus *Chorus* Gray, 1847 (type species: *Chorus giganteus* (Lesson, 1831)), from Chile. Both genera have a labral tooth corresponding to a basal groove, but *Chorus* lacks the posterior notch and parietal rib characteristic of *Testallium,* the replacement name for *Gastridium* Sowerby, 1846. In *Chorus* as in other muricids, the spiral sculpture of the last whorl increases in prominence from the base to the shoulder rather than from the shoulder to the base as in *Testallium* and other pseudolivids. The cords of *Chorus* are widely separated and rounded, not crowded as in *Testallium.*

Testallium differs from *Pseudoliva* by having the last whorl covered with fine spiral sculpture instead of being smooth, by having the base of the last whorl distinctly constricted (that is, with a concave lateral profile) instead of being evenly tapered, by having a prominent, keel-like siphonal fasciole instead of a low, rounded one, by the very limited development of callus, and by having the lower part of the outer lip distinctly crenulated. It differs from *Sulcobuccinum* by the lower position of the pseudolivid groove on the last whorl, by the limited development of callus, and by the presence of a parietal rib at the adapical end of the inner lip. *Testallium* is very similar to *Macron.* Whereas the inner side of the outer

lip of *Testallium* is smooth, that of *Macron* is sculptured with riblets (lirae).

There is considerable intraspecific variation in the degree of development of the shoulder. In some forms of *T. cepa* and in *T. voluta,* the shoulder may be developed as a raised ridge in the mature shell; whereas in other specimens of *T. cepa,* the upper part of the whorl is rounded (see Vermeij & DeVries, 1997).

Included in *Testallium* are *T. cepa* from the Early Miocene of southern Peru to southern Chile, *T. voluta* from the Heath Formation (?Early Miocene) of northern Peru, and *T. escalonia* from the Late Pliocene of Chile. *Testallium voluta,* which Olsson (1932) originally described as a species of *Acanthiza (Chorus),* differs from the other two species by having axial ribs on the spire whorls. Olsson's *Acanthiza* was presumably a misspelling of *Acanthina,* another ocenebrine muricid genus with a labral tooth (see Vermeij & DeVries, 1997).

Genus *Macron* H. & A. Adams, 1853

Type species: *Pseudoliva (Macron) kellettii* A. Adams, 1854 (= *Buccinum aethiops* Reeve, 1847).

Synonym:
Macroniscus Thiele, 1929 (Type species: *Macron lividus* A. Adams, 1855).

Diagnosis: Shell small to large, maximum height 20 to 100 mm, ovate; protoconch paucispiral; spire relatively high, last whorl comprising 68 to 74% of total shell height; sutures appressed to deeply impressed; last whorl rounded or shouldered above, little or not constricted basally; spiral sculpture consisting of weak to very prominent cords decreasing in strength from base to shoulder; axial sculpture absent; pseudolivid groove situated low in last whorl; outer lip planar, usually with distinct labral tooth (obsolete in *M. lividus*), strongly crenulated below; inner side of outer lip lirate; posterior notch weak; aperture ovate in most species, its height-to-breadth ratio 1.9 to 4.1 (narrowly elongate in *M. merriami*); columella with weak fold at entrance of siphonal canal; columellar and parietal callus of very limited extent; siphonal fasciole prominent, bounded above by keel; anterior notch deep; umbilicus present or absent.

Stratigraphic and geographic distribution: Early Miocene to Recent, warm-temperate northeastern Pacific; ?Early Pliocene, Japan.

Discussion: *Macron* has remained a taxonomic enigma ever since H. & A. Adams (1853:132) introduced it as a subgenus of *Pseudoliva* in the muricid subfamily Purpurinae. Adams (1855) and Sowerby (1859) maintained this assignment. Fischer (1884) referred *Macron* to the Buccinidae, along with other Pseudolividae. Cossmann (1901) and Melvill (1903) refined this assignment by referring the genus to the Latrunculinae or Eburninae (= Babyloniinae), and noted that, whereas *Macron* has an unguiculate operculum with a terminal nucleus, *Pseudoliva* has a purpuroid operculum with a laterally

placed nucleus. Grant and Gale (1931) re-examined the opercula of the two genera and concluded that both are characterized by a terminal opercular nucleus. They therefore reaffirmed the close relationship between *Macron* and *Pseudoliva*. Thiele (1929) described the radula of *M. trochlea* (Gray) (= *M. aethiops*) and of *M. lividus*, and assigned the genus to the Buccinidae. In this assignment, he was followed by Wenz (1938–44), Glibert (1963), Addicott (1970), Keen (1971), and Abbott (1974).

Yuri Kantor (personal communication) suggests that the radula of *Macron* is very similar to that of the Nassariidae. As illustrated by Thiele under the name *M. trochlea*, the rachidian tooth is multicuspidate with small cusps, and the lateral teeth are tricuspidate. The pseudolivid radula, by contrast, either has a multicuspidate rachidian and unicuspidate marginal teeth or a tricuspidate rachidian with very large cusps and bicuspidate marginal teeth (Kantor, 1991). The shell characters of *Macron*, however, differ widely from those of Nassariidae. The genus *Nassarius* Duméril, 1906, and related taxa (see Cernohorsky, 1984) are characterized by determinate growth, and by a polished outer lip with an anterior sinus. *Macron*, by contrast, has a simple, sharp-edged, outer lip indicating indeterminate growth and lacking any trace of an anterior sinus.

The pseudolivid affinities of *Macron* are strongly supported by shell characters. These include a thick periostracum, pseudolivid groove and corresponding labral tooth (obsolete in *M. lividus*), sharp-edged simple outer lip, posterior notch, and spiral sculpture most strongly expressed near the base. The only similar genus that has traditionally been referred to the Buccinidae is *Triumphis*, which differs from *Macron* chiefly by the absence of the pseudolivid groove and labral tooth. With the transfer of *Triumphis* to the Pseudolividae (see below), there is no other buccinid genus that closely resembles *Macron*.

Macron is most similar to *Testallium*, from which it differs principally in having the inner side of the outer lip sculptured by nine to seventeen riblets (lirae). In *Testallium*, the inner side of the outer lip is smooth.

The middle Miocene species *Macron merriami* from the Temblor Formation of southern California may represent an evolutionary link with *Testallium*. This species has very weak spiral sculpture, a rounded (not shouldered) last whorl, appressed suture, weakly constricted base, and an unusually narrow aperture (height-to-breadth ratio 4.1). Because the aperture of the holotype is filled with matrix, the presence of lirae on the inner side of the outer lip cannot be ascertained. The species could therefore be assigned to either *Testallium* or *Macron*. I retain it in *Macron* on the basis of its geographic provenance (California instead of western South America).

Another species, *Macron hartmanni*, may link *Macron* with the genus *Triumphis*. This species, described by Hertlein and Jordan (1927) from the San Ignacio Formation (middle to late Miocene; see Smith, 1984) of Baja California Sur, Mexico, resembles *Triumphis* in having a raised, keel-like shoulder, but differs from that genus by having six to ten low, flattened cords on the last whorl and by the presence of a blunt but distinct labral tooth at the end of a pseudolivid groove. Addicott (1970) provisionally assigned *M. hartmanni* to *Nicema*, a taxon that has occasionally been considered a subgenus of *Triumphis* but that is here assigned to the buccinid subfamily Photinae (see below). *Nicema* lacks the labral tooth and pseudolivid groove of *Macron*. I therefore agree with Hertlein and Jordan (1927) that their species should be referred to the genus *Macron*.

The type species of *Macron*, *M. aethiops*, is the largest, most heavily sculptured living member of the Pseudolividae, attaining a height of 100 mm. The expression of spiral sculpture above the pseudolivid groove is highly variable even within populations. In typical *M. aethiops*, seven thick, flattened or rounded cords with very deep interspaces lie between the pseudolivid groove and the shoulder. In the *kellettii* form, only the lowest one or two of these cords are expressed. All forms have a deeply impressed, canaliculate suture, and all have fifteen or more lirae on the inner side of the outer lip. In the living fauna, *M. aethiops* occurs on the Pacific coast of Baja California from just south of Ensenada to just south of Bahia Magdalena. There appears to be a geographically isolated population in the Gulf of California. The species is not represented on the southern part of the Baja California peninsula. My examination of a specimen reported by Mulliner (1996) from Isla Danzante in the Gulf of California indicates that this specimen falls well within the limits of variation of the species as a whole. With only one cord above the pseudolivid groove, the specimen from Isla Danzante belongs to the *kellettii* form of *M. aethiops*. It is unusual among pseudolivids in that the left (leading) edge of the inner lip has a distinct margin. In the fossil record, *M. aethiops* occurs in the lower Olcese sand (middle Miocene) and the San Pedro beds (Early Pleistocene) of southern California (Grant & Gale, 1931; Addicott, 1970).

Thiele (1929) proposed the subgenus *Macroniscus* for *Pseudoliva* (*Macron*) *livida* A. Adams, 1855, a small species from the Pleistocene and Recent of southern California. It differs from other species of *Macron* by its small size (maximum height 18.6 mm), appressed rather than channeled suture, obsolete pseudolivid groove and labral tooth, and very weak basal spiral cords. Although *M. lividus* does not closely resemble the large, strongly sculptured *M. aethiops*, several species are morphologically intermediate. These include *M. orcutti*, *M. mcleani* n. sp. (see below), and an early Miocene species, *Macron constrictus*, described by Gibson-Smith, Gibson-Smith, and Vermeij (1997) from the Cantaure Formation of Venezuela. This less sculptured group does not merit distinction as a subgenus or genus *Macroniscus*, which I therefore consider a subjective synonym of *Macron*.

Besides the living and fossil species of *Macron* from the warm-temperate northeastern Pacific and the early Miocene species from Venezuela in the western Atlantic,

Figures 16–17. *Macron mcleani* new species; Bahia Gonzaga, Gulf Coast, Baja California Norte, Mexico; LACM 37-119. Shell height 23.1 mm.

there is one species from the early Pliocene of Japan that has been tentatively referred to *Macron.* Chinzei (1959) named *"Macron" nipponensis* on the basis of a single, thick-shelled specimen from the Kubo Formation of Honshu. It is characterized by thirteen spiral cords on the last whorl and five cords on spire whorls, the cords increasing in strength toward the constricted base. Chinzei (1959) mentions neither a pseudolivid groove nor a labral tooth. The outer lip, whose inner side is ornamented with ten denticles, is exceptionally thick and is posteriorly notched. An umbilicus is absent. *"Macron" nipponensis* differs from *Macron* by the absence of a labral tooth and pseudolivid groove and by the presence of denticles rather than brief lirae on the inner side of the outer lip. If the species belongs to the Pseudolividae, it may have paralleled *Triumphis* in having lost the pseudolivid groove and labral tooth.

For the time being, I retain *M. nipponensis* in the genus *Macron.*

Macron mcleani, new species
(Figures 16–17)

Diagnosis: *Macron* with smooth, rounded whorl, appressed suture, nine lirae on inner side of outer lip, narrow aperture, and fibrous periostracum.

Description: Shell ovate-fusiform, consisting of about five teleoconch whorls; spire moderately high, last whorl comprising 68% of total shell height; suture appressed; last whorl gently and evenly rounded on upper part, very weakly constricted at base; spiral sculpture consisting of three low cords on base, above which is a distinct (pseudolivid) groove; axial sculpture absent; outer lip planar,

with three strong crenulations on anterior sector below a blunt labral tooth; inner side of outer lip with nine brief lirae; posterior end of aperture with parietal rib; inner lip appressed, with a distinct fold at entrance of siphonal canal; aperture elongate, its height-to-breadth ratio 3.1; siphonal fasciole low, rounded; anterior siphonal notch deep; umbilicus absent; periostracum fibrous; shell brown, interior of aperture white.

Holotype: Height 23.1 mm, diameter 11.9 mm, aperture height 15.6 mm, aperture width 5.1 mm. LACM 2812.

Type locality: Willard Point, Bahia Gonzaga, Baja California Norte, Mexico, 29°48' N, 114°23' W, two to three fathoms in sand.

Etymology: I take great pleasure in naming this species for James H. McLean, great authority on the living mollusks of the northeastern Pacific, who brought this species to my attention.

Remarks: *Macron mcleani* is most similar to *M. lividus.* Both species have a distinctly fibrous periostracum, a broadly fusiform shape, obsolete spiral sculpture, and an appressed suture. *Macron mcleani* differs from *M. lividus* by having a distinct rather than an obsolete labral tooth, by having nine strong lirae instead of nine to twelve very faint lirae on the inner side of the outer lip, and by having a much narrower aperture (apertural height-to-width ratio 3.1 as compared to 2.3 to 2.5 in *M. lividus*). Other relatively smooth species of *Macron* (*M. orcutti* and the early Miocene species being described by Gibson-Smith et al., 1997) have a relatively broader

aperture and a larger number of lirae (thirteen to seventeen) than *M. mcleani*.

Genus *Triumphis* Gray, 1857

Type species: *Buccinum distortum* Wood, 1828, by monotypy.

Diagnosis: Shell large, maximum height 63 mm, ovate; protoconch paucispiral, consisting of 2.25 to 2.5 smooth whorls; spire relatively high, last whorl comprising 66 to 75% of total shell height; spire whorls flattened, sutures appressed; last whorl rounded above in young stages, but with a strong, ridge-like shoulder during final growth stages; basally not constricted; spiral sculpture consisting of two or three cords on spire whorls, one or two low, rounded, below shoulder on last whorl, and five stronger basal cords on last whorl; axial sculpture confined to spire whorls, consisting of ten rounded ribs per whorl; pseudolivid groove and labral spine absent; outer lip more or less planar, its base sharply crenulated at terminations of grooves between basal cords; posterior notch weak, often obsolete in mature shells; inner side of outer lip with ten to eleven long lirae; aperture ovate to elongate-ovate, its height-to-breadth ratio 2.1 to 2.8; posterior end of aperture constricted by massive, rounded parietal ridge; columella with three or four superficial ridges on upper part, and with weak fold at entrance of siphonal canal; columellar and parietal callus often thick, but of very limited extent; siphonal fasciole low, rounded; anterior siphonal notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Early Miocene, southern California; Recent, tropical eastern Pacific.

Discussion: All previous authors who have concerned themselves with the classification of *Triumphis* have assigned it to the Buccinidae. When introducing *Triumphis*, Gray (1857:15) referred his new genus to the Pisaniana (= Pisaniinae), a group which, along with other buccinid subfamilies, he assigned to a greatly expanded Muricidae. Fischer (1884) treated it as a subgenus of *Cominella* Gray, 1850. Cossmann (1901) affirmed this assignment by referring the genus to the subfamily Cominellinae (= Photinae). Thiele (1929) and Wenz (1938–44), however, considered *Triumphis* a subgenus or section of *Cantharus* Röding, 1798, a genus usually assigned to the subfamily Pisaniinae (see Cernohorsky, 1971, 1975). Keen (1971) recognized it as a full genus, but she did not specify where in the family it belongs.

Assignment of *Triumphis* to the Photinae is precluded on three grounds. A heavy periostracum of the kind seen in *Triumphis* is not known in any member of the Photinae, in which the periostracum is either absent or very thin. The outer lip of *Triumphis* has two characteristics inconsistent with assignment of the genus to Photinae. In *Triumphis*, the edge of the outer lip is sharp, and the smooth surface of the inner side of the outer lip does not cross the edge to the outer side. In most Photinae, by contrast, the edge of the outer lip is polished, because the inner layer minutely extends across the edge to the outer side. The anterior part of the outer lip above the siphonal notch lacks a sinus in *Triumphis*. Instead, this part of the lip is planar and bears very strong crenulations. In most Photinae, the outer lip is medially convex, and there is a variably developed concave sinus between the convex sector above and the anterior siphonal notch below. This sinus is so prominent in some genera that it is occasionally referred to as a stromboid notch to emphasize the superficial resemblance with the anterior part of the outer lip in the Strombidae. The sinus in the Photinae is not strongly serrated as is the basal sector of the outer lip in *Triumphis*. *Triumphis* superficially resembles some members of the Pisaniinae, including *Cantharus* and related genera, in possessing a thick, persistent periostracum, and by having an unreflected, sharp-edged outer lip; but it differs in characters of shell sculpture and in the profile of the outer lip. In *Triumphis*, the strength of spiral sculpture increases from the shoulder to the base. This condition is typical of the Pseudolividae as well as of many other neogastropod groups including the buccinid subfamilies Photinae and Siphonaliinae, and the families Nassariidae, Fasciolariidae, Costellariidae, and clades within the Toxoglossa, among others. This condition contrasts with the situation in the Pisaniinae as well as in most Muricidae, in which spiral sculptural elements increase in prominence from the base to the whorl shoulder. The outer lip of immature and most mature *Triumphis* is characterized by a notch at the junction with the penultimate whorl. Such a notch is absent in Pisaniinae. In the latter subfamily, the outer lip has a convex profile in its medial sector, and a broad, shallow sinus on its upper half. The outer lip of *Triumphis* is strongly crenulated at its edge only along its lower half, as in most other Pseudolividae, whereas in the Pisaniinae it is crenulated along its entire length.

I assign *Triumphis* to the Pseudolividae because of the following combination of characters: persistent periostracum, planar sharp-edged outer lip without anterior sinus, presence of posterior notch, spiral sculpture strongest near base, and outer lip crenulated at ends of basal spiral grooves. *Triumphis* clearly diverges from most other pseudolivids by the absence of a pseudolivid groove and corresponding labral tooth. The point along the edge of the outer lip at which crenulations begin, however, corresponds to the position of the pseudolivid groove and labral tooth in such genera as *Macron* and *Testallium*. Thiele's (1929) description of the rather generalized radula of *Triumphis* is also consistent with placement of *Triumphis* in the Pseudolividae. Anatomical data and molecular sequences will be needed to confirm the phylogenetic affinities of *Triumphis*.

Addicott (1970) referred a single, poorly preserved specimen from the Middle Miocene Olcese Sand of southern California to the genus *Triumphis*. If additional material confirms this assignment, *Triumphis* would have

a record dating back to the middle Miocene. The only other species, *T. distorta*, is known only from the Recent tropical eastern Pacific, where it ranges from El Salvador to northern Peru.

Kilburn and Tankard (1975) described *Triumphis dilemma* from early Pliocene strata in Cape Province, South Africa (see also Kensley and Pether, 1986). Elsewhere (Vermeij, 1997), I have shown that this species is not closely related to *Triumphis*, and I proposed a new genus for it in the buccinid subfamily Photinae.

TAXA EXCLUDED FROM PSEUDOLIVIDAE

Several genera and species included by previous authors in the Pseudolividae or Pseudolivinae or in taxa here assigned to that family do not belong in this group. Some of these are treated below. A few western North American Paleogene species assigned to *Pseudoliva* by previous authors were already excluded by Squires (1989) and will not be discussed further here.

Material examined is listed in Appendix 2. I provide diagnoses for *Melapium*, *Nicema*, and *Seymourosphaera*, because important shell characters of these genera have not been noted previously. My conclusions about the genus *Austrosphaera* are surmised from Oleinik and Zinsmeister's (1996) paper. The Cretaceous genera *Fulgerca*, *Hydrotribulus*, and *Ptychosyca* were so well described by Sohl (1964a, b) that diagnoses for them are superfluous. The important shell attributes of these genera are mentioned below in the discussions of these taxa.

Genus *Nicema* Woodring, 1964

Type species: *Nicema amara* Woodring, 1964, by original designation.

Diagnosis: Shell moderately large, maximum height 57 mm, broadly fusiform; protoconch paucispiral; spire consisting of five to seven teleoconch whorls; spire moderately high, last whorl comprising 68 to 82% of total shell height; sutures appressed, increasingly deep in later growth stages; last whorl rounded or weakly shouldered above, the shoulder a raised ridge in mature specimens of some species; last whorl basally constricted; spiral sculpture consisting of about seven weak cords on spire whorls, and of up to seven cords on and just above basal constriction of last whorl; axial sculpture consisting of eight to ten rounded folds on spire whorls, obsolete or absent on last one or two whorls; pseudolivid groove and labral tooth absent; outer lip medially convex downward, with adapical concave sinus and weak posterior notch; lower sector of outer lip crenulated by ends of grooves between basal cords; upper concave sector of outer lip with smooth edge; inner side of outer lip briefly lirate in adult; aperture elongate-ovate, its height-to-breadth ratio 2.8 to 2.9; inner lip smooth, adherent or very slightly erect; columellar callus very limited in extent; columella smooth, concave, with basal fold at entrance of siphonal canal; parietal rib present; siphonal fasciole

prominent, sculptured with spiral threads and bounded adapically by keel; siphonal canal dorsally recurved, with deep anterior notch; umbilicus absent or represented by very narrow slit.

Stratigraphic and geographic distribution: Late Miocene to Recent, tropical eastern Pacific; Late Miocene, Atlantic Panama.

Discussion: Woodring (1964) proposed the genus *Nicema* for several late Miocene buccinids from tropical America. Besides the type species, *N. amara* from the Gatun Formation of Panama, he included *N. guttifera* (Grzybowski, 1899) from northern Peru and *N. predistorta* (Marks, 1951) from the Daule beds of Ecuador. Olsson (1964) considered *Nicema* as a subgenus of *Northia* Gray, 1847, and added his new species *N. noctua* and *N. venada* from the Miocene of Ecuador. Keen (1971) included *Nicema* as a subgenus of *Triumphis*, and added still another species, *N. subrostrata* (Wood, 1828) from the tropical eastern Pacific. Finally, Addicott (1970) tentatively referred *Macron hartmanni* Hertlein & Jordan, 1927, to *Nicema*. I have retained the latter species in *Macron*. All authors except Olsson (1964) considered *Nicema* to be closely related to *Triumphis*.

Despite its morphological similarity to *Triumphis*, *Nicema* may belong to the buccinid subfamily Photinae rather than to the Pseudolividae. *Nicema* resembles *Triumphis* in having a low spire (last whorl comprising 79 to 82% of total shell height in *N. subrostrata*, 68% in *N. noctua*, 73% in *T. distorta*), axial sculpture confined to the spire whorls, an adapical notch, strong rounded parietal rib, adherent smooth inner lip, lirate outer lip, and a persistent periostracum. The most conspicuous differences reside in the spiral sculpture and the shape of the outer lip. In *Nicema*, the constricted basal part of the last whorl is adorned with fine threads, and stronger cords occur above this sector. In *Triumphis*, the strongest sculpture (of five cords) occurs on the unconstricted base. The outer lip of *Triumphis* is essentially planar in profile, whereas that of *Nicema* is medially convex and adapically characterized by a broad, concave, smooth-edged sinus below a shallow notch where the outer lip joins the penultimate whorl.

Characters of the outer lip and the external shell sculpture support Olsson's (1964) suggestion that *Nicema* is related to *Northia* and other genera in the buccinid subfamily Photinae. The only characteristic inconsistent with this assignment is the absence of a sinus on the lower half of the outer lip. Such a sinus characterizes most photines, but not *Nicema*. Anatomical observations on the living *N. subrostrata* will be needed to confirm my assignment of *Nicema* to the Photinae.

In addition to the species assigned to *Nicema* by Woodring (1964), Olsson (1964), and Keen (1971), the genus *Nicema* includes *Clavella solida* Nelson, 1870, from the Late Miocene of northern Peru (see also Vermeij & DeVries, 1997). This species, which Olsson (1932) assigned to the muricid subgenus *Acanthiza* (*Chorus*), has eight to ten strong axial ribs on the spire

whorls, a weakly constricted base, strong fasciolar ridge, and narrow umbilical chink, has the shoulder raised into a ridge in the adult stage. Olsson (1932) perceived a pseudolivid groove, and compared his specimens of *N. solida* to *Gastridium* (= *Testallium*) *cepa* and *Acanthiza (Chorus) voluta* Olsson, 1932, a species here assigned to *Testallium*. My examination of the holotype of *Clavella solida* failed to reveal a pseudolivid groove, and Nelson (1870) did not mention such a feature in his accurate original description of the species. Instead, the last whorl shows an abrupt abapical narrowing near its base. This abrupt narrowing is not like the deeply concave basal constriction of *Nicema subrostrata*, in part because the siphonal canal of *Clavella solida* is not dorsally recurved as it is in other species of *Nicema*, but in other respects Nelson's species resembles members of *Nicema*.

Jung (1995) named the genus *Judaphos* for *J. imparabilis* Jung, 1995, a Late Miocene species from the Pacific coast of Costa Rica. *Judaphos* closely resembles *Nicema* but differs from the latter genus by being more slender and having a less prominent siphonal fasciole. It is possible that *Judaphos* forms a link between *Northia* and *Nicema*.

Genus *Melapium* H. & A. Adams, 1853

Type species: *Pirula lineata* Lamarck, 1822, subsequent designation by Cossmann, 1901.

Diagnosis: Shell large, maximum height 100 mm, globose; protoconch large, paucispiral; spire very low, last whorl comprising 97% or more of total shell height; last whorl evenly rounded above, strongly constricted basally; spiral sculpture consisting of about six low cords on basal constriction; axial sculpture consisting of distinct growth lines; pseudolivid groove and labral tooth absent; outer lip simple, gently and evenly convex; inner side of outer lip smooth; posterior notch weak but present; aperture ovate, its height-to-breadth ratio 2.1; columella with strong fold at entrance of siphonal canal; inner lip adherent; adapical end of inner lip with strong parietal tooth; siphonal fasciole well developed, bounded adapically by prominent keel; siphonal canal dorsally strongly recurved; anterior siphonal notch deep; umbilicus absent; parietal and columellar callus well developed, rendering apertural side of last whorl flattened, but callus not extending onto spire.

Stratigraphic and geographic distribution: Early Pliocene to Recent, southern Africa.

Discussion: The genus *Melapium* was placed in the Strepturidae by Cossmann (1901) and in the Olividae (Pseudolivinae) by Thiele (1929), Wenz (1938–44), and Kilburn (1989). A study of shell and anatomical characters persuaded Kantor (1991) to place *Melapium* in its own family Melapiidae. According to Kantor (1991), *Melapium* differs from Pseudolividae by the absence of accessory salivary glands and of the operculum, and by having the opening of the radular diverticulum to the buccal cavity at the tip rather than at the base of the proboscis. The accessory esophageal gland of *Melapium* is hypertrophied.

The shell of *Melapium* also differs from that of the Pseudolividae. The pseudolivid groove and labral tooth are absent in *Melapium*, and the base of the columella is marked by a prominent fold at the entrance of the siphonal canal. The siphonal canal, moreover, is long and strongly recurved dorsally.

Given the characters of the shell of *Melapium*, I tentatively agree with Cossmann (1901) in assigning the genus to the Strepturidae. *Melapium* differs from the type genus *Strepsidura* Swainson, 1840, by the absence of axial sculpture, and by the presence of a strong parietal tooth. A considerable stratigraphic gap exists between the last appearance of *Strepsidura* in the Late Eocene and the first Pliocene appearance of *Melapium*. Considering the poor pre-Pliocene fossil record in South Africa, such a stratigraphic hiatus does not constitute strong evidence against a phylogenetic link between the Paleogene Strepturidae and the Late Neogene *Melapium*. If *Melapium* does prove to belong to the Strepturidae, the name Melapiidae Kantor, 1991, would fall as a subjective junior synonym of Strepturidae Cossmann, 1901.

The genus *Melapium* is represented by two living species, *M. lineatum* from the temperate coast of South Africa, and *M. elatum* (Schubert & Wagner, 1829) from Natal and Mozambique. Kensley and Pether (1986) additionally recognize two fossil species, *M. patersonae* Bullen Newton, 1913, from the Neogene of Bredasdorp; and *M. hawthornei* Kensley & Pether, 1986, from the 30 m and 50m levels (Early to Middle Pliocene) at Hondeklip Bay, Cape Province, South Africa.

Genus *Austrosphaera* Camacho *in* Furque & Camacho, 1949

Type species: *Austrosphaera glabra* Camacho *in* Furque & Camacho, 1949.

Discussion: Oleinik and Zinsmeister (1996) have given a brief account of this Late Cretaceous and earliest Paleocene genus from Patagonia and Tierra del Fuego, Argentina. The shell is thick, low-spired, and semi-ovate, with short, shallow anterior and posterior canals and a poorly developed siphonal fasciole. Although spiral sculpture, a pseudolivid groove, and a labral tooth are absent, Oleinik and Zinsmeister (1996) assigned *Austrosphaera* with doubt to the buccinid subfamily Pseudolivinae. I have not examined any material of *Austrosphaera*, but on the basis of great similarity with *Seymourosphaera* (see below), I tentatively exclude *Austrosphaera* from the Pseudolividae. Just where this genus should be assigned remains unclear.

Genus *Seymourosphaera* Oleinik & Zinsmeister, 1996

Type species: *Seymourosphaera bulloides* Oleinik & Zinsmeister, 1996, by original designation.

Diagnosis: Shell of medium size, maximum height 41 mm, broadly fusiform; protoconch large, paucispiral, smooth; teleoconch consisting of four to five whorls separated by impressed suture; spire low, last whorl comprising 79 to 94% of total shell height; last whorl evenly rounded on upper part, weakly constricted at base; spiral sculpture consisting of very weak, low, fine cords, best expressed on spire whorls and on upper part of last whorl, but often absent on last whorl and not expressed on base; axial sculpture absent; pseudolivid groove and labral tooth absent; outer lip of mature shell abaxially expanded, weakly convex, slightly thickened and smooth on inner side; posterior notch weak but present; aperture broadly ovate, its height-to-breadth ratio 1.9 to 2.3, adapically narrowed, but outer lip not adapically extended; columella rounded, its profile sigmoid, smooth, without basal fold; parietal callus ventrally thick, extending partly onto spire in some species; inner lip adherent; parietal rib absent; siphonal fasciole absent or low and rounded; anterior siphonal notch very shallow; umbilicus absent.

Stratigraphic and geographic distribution: Early Paleocene, Seymour Island. Antarctic Peninsula.

Discussion: The above diagnosis is based on my examination of paratypes of *S. bulloides* and all the other three members of the genus, very kindly sent to me by Anton Oleinik. When they proposed the genus *Seymourosphaera*, Oleinik and Zinsmeister tentatively assigned it to the buccinid subfamily Pseudolivinae, although they noted that a pseudolivid groove and labral tooth are absent. Two characters are inconsistent with assignment of *Seymourosphaera* to the Pseudolividae. Spiral sculpture is best developed on the upper part of the whorl, and therefore does not increase in prominence abapically as it does in the Pseudolividae. The outer lip of *Seymourosphaera* is abaxially expanded and is somewhat thickened on its smooth inner side; it therefore indicates determinate growth. Pseudolivids never show abaxial expansion of the adult outer lip and apparently continue to grow in the spiral direction throughout life.

Just how *Seymourosphaera* should be classified remains unclear. Despite superficial resemblance to *Melapium*, *Seymourosphaera* is unlikely to belong to the Streptruidae. Members of that family have spiral sculpture increasing in prominence abapically, have a strong basal columellar fold, and display indeterminate growth. *Seymourosphaera* may belong to a large Paleogene complex of buccinoid gastropods with low-spired shells that have no Neogene or Recent relatives.

Oleinik and Zinsmeister (1996) named four species of *Seymourosphaera*, all from a restricted interval of the Early Paleocene Sobral Formation and the uppermost part of the underlying Lopez de Bertodano Formation of Seymour Island, Antarctic Peninsula. All the species are extremely similar to each other, varying only in spire height and in the degree of persistence of the very weak spiral sculpture on the last whorl. I strongly suspect that the three species confined to the Sobral Formation (*S.

depressa, S. subglobosa, and *S. bulloides*) are a single species, which would then be known as *S. bulloides*. The fourth and oldest species (*S. elevata*), known from the uppermost Lopez de Bertodano Formation as well as from the Sobral Formation, differs from the others by having a higher spire of five instead of four whorls. It may be a distinct species.

Genus *Fulgerca* Stephenson, 1941

Type species: *Fulgerca venusta* Stephenson, 1941 (=? *Pseudoliva? attenuata* Wade, 1926; see Sohl, 1964b), by original designation.

Discussion: Three genera from the Late Cretaceous of the Atlantic and Gulf Coastal Plain of the United States have often been included in the Pseudolividae, probably because they possess a labral tooth (see Sohl, 1964a, b). One of these is the Santonian to Maastrichtian genus *Fulgerca*. The labral tooth is formed at the end of a fasciolar band at the tapering, unconstricted base of the gently rounded last whorl. The spire is high, the last whorl comprising 50% or more of the total shell height. Sculpture consists of fine spiral and axial elements. Sohl (1964a, b) gives a thorough overview of the group.

Exclusion of *Fulgerca* from the Pseudolividae is supported by several characters, including the high spire and the formation of the labral tooth at the termination of a fasciolar band instead of at the end of a groove above the fasciole. Where *Fulgerca* should be assigned remains unresolved. Ponder (1973) suggested an affinity with the Colubrariidae (now often considered part of the buccinid subfamily Pisaniinae; see Beu & Maxwell, 1987), perhaps because of the elongate fusiform shape, high spire, and finely cancellate sculpture of *Fulgerca*. The labral tooth formed at the end of the fasciolar band would, however, be unique among Pisaniinae. For the present, I prefer to keep the familial assignment of *Fulgerca* open.

ACKNOWLEDGMENTS

LITERATURE CITED

Abbott, R. T. 1974. American Seashells. 2nd edition. New York, Van Nostrand Reinhold Co. 661 pp.

Adams, A. 1855. Descriptions of new genera and species of gastropodous Mollusca. Proceedings of the Zoological Society of London (1853):182–186.

Adams, H. and A. Adams. 1853. The genera of Recent Mollusca; arranged according to their organization. Vol. 1. London, John Van Voorst.

Addicott, W. O. 1970. Miocene gastropods and biostratigraphy of the Kern River area, California. United States Geological Survey Professional Paper 642:1–174.

Adegoke, O. S. 1977. Stratigraphy and paleontology of the Ewekoro Formation (Paleocene) of southwestern Nigeria. Bulletins of American Paleontology 71:1–379.

Albanesi, C. and G. Busson. 1974. Gastéropodes du Cretacé supérieur de l'extréme-sud tunisien et de la région du Tinrhert (Sahara Algérien). Rivista Italiana di Paleontologia i Stratigrafia 80:251–342.

Allmon, W. D. 1990. Review of the *Bullia* group (Gastropoda: Nassariidae) with comments on its evolution, biogeography, and phylogeny. Bulletins of American Paleontology 99:1–179.

Bandel, K. 1993. Caenogastropoda during Mesozoic times. Scripta Geologica Special Issue 2:7–56.

Beu, A. G. and P. A. Maxwell. 1987. A revision of the fossil and living gastropods related to *Plesiotriton* Fischer, 1884 (family Cancellariidae, subfamily Plesiotritoninae n. subfam.), with an appendix: genera of Buccinidae Pisaniinae related to *Colubraria* Schumacher, 1817. New Zealand Geological Survey, Paleontological Bulletin 54:1–140.

Beu, A. G. and P. A. Maxwell. 1990. Cenozoic Mollusca of New Zealand. New Zealand Geological Survey, Paleontological Bulletin 58:1–518.

Beyrich, E. 1854. Die Conchylien des Norddeutschen Tertiärgebirges. Zweite und Dritte Lieferung. Berlin, Wilhelm Hertz. 81–176.

Blanckenhorn, M. 1927. Die fossilen Gastropoden und Scaphopoden der Kreide von Syrien-Palästina. Palaeontographica 69:111–186.

Böhm, J. 1926. Über Tertiäre Versteinerungen von den Bogenfelser Diamantenfeldern. *In* E. Kaiser (ed.), Die Diamantenwuste Süd-west-Afrikas. Band II. Berlin, Verlag von Dietrich Reimer (Ernst Vohsen), pp. 55–87.

Bouchet, P. & G. J. Vermeij. 1998. Two new deep-water Pseudolividae (Neogastropoda) from the south-west Pacific. The Nautilus 111(2):47–52.

Bouchet, P. and A. Warén. 1985. Revision of the northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca: Gastropoda). Bollettino Malacologico Supplemento 1:123–296.

Cernohorsky, W. O. 1971. Indo-Pacific Pisaniinae (Mollusca: Gastropoda) and related buccinid genera. Records of the Auckland Institute Museum 8:137–167.

Cernohorsky, W. O. 1975. Supplementary notes on the taxonomy of buccinid species of the subfamily Pisaniinae (Mollusca: Gastropoda). Records of the Auckland Institute and Museum 12:175–211.

Cernohorsky, W. O. 1984. Systematics of the family Nassariidae (Mollusca: Gastropdoa). Bulletin of the Auckland Institute and Museum 14: 1–356.

Chinzei, K. 1959. Molluscan fauna of the Pliocene Sannohe Group of northeast Honshu, Japan. 1. The faunule of the Kubo Formation. Journal of the Faculty of Science, University of Tokyo, Section II, 12: 103–132.

Clark, B. L. and J. W. Durham. 1946. Eocene fossils from the Department of Bolívar, Colombia. Geological Society of America Memoir 16:1–126.

Conrad, T. A. 1865. A catalogue of the Eocene and Oligocene Testacea of the United States. American Journal of Conchology 1:1–35.

Coquand, H. 1862. Géologie et paléontologie de la région sud de la province Constantine. Marseille: Arnaud et Cie.

Cossmann, M. 1889. Catalogue illustré des coquilles fossiles de l'Eocéne des environs de Paris. Annales de la Societé Royale Malacologique de Belgique 24 (4éme Serie, 4):3–381.

Cossmann, M. 1901. Essais de Paloconchologie comparée. Paris: M. Cossmann, 293 pp.

Dall, W. H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80) by the U. S. Coast Survey Steamer "Blake," Lieut. Commander C. D. Sigsbee, U.S.N., and Commander J. R. Hartlett, U.S.N., commanding. XXIX. Report on the Mollusca, Part II, Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology at Harvard College 18:1–492.

DeVries, T. J. and G. J. Vermeij. 1997. *Herminespina*: new genus of Neogene muricid gastropod from Peru and Chile. Journal of Paleontology 71:610–615.

Dockery, D. T. III. 1977. Mollusca of the Moodys Branch Formation Mississippi. Bulletin of the Mississippi Geological, Economic and Topographic Survey (Jackson) 120:1–212.

Dockery, D. T. III. 1980. The invertebrate macropaleontology of the Clark County, Mississippi, area. Mississippi Department of Natural Resources, Bureau of Geology, Bulletin 122:1–387.

Douvillé, H. 1933. Le Tertiaire de Loanda. Boletim do Museo e Laboratório Mineralógico e Geológico da Universidade de Lisboa 1 (Ser. 1):93–118.

Eames, F. E. 1957. Eocene Mollusca from Nigeria: a revision. Bulletin of the British Museum (Natural History), Geology 3:23–70.

Etayo Serna, F. 1979. La fauna de moluscos del Paleoceno de Colombia: moluscos de una capa del Paleoceno de Manantial (Guajira). Boletin de Geología, Universidad Industrial de Santander, Bucaramanga (Colombia) 13(27):5–55.

Fischer, P. 1884. Manuel de Conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles. Fascicule VII. Paris, F. Savy. 609–688.

Gardner, J. 1945. Mollusca of the Tertiary formations of northeastern Mexico. Geological Society of America Memoir 11:1–332.

Gibson-Smith, J., W. Gibson-Smith, and G. J. Vermeij. 1997. Pacific Mexican Affinities of New Species of the Gastropod Genera *Macron* (Pseudolividae) and *Neorapana* (Muricidae) from the Cantaure Formation (Early Miocene) of Veneznela. The Veliger 40(4):358–363.

Glibert, M. 1960. Les Volutacea fossiles du Cénozoïque étranger des collections de l'Institut Royal des Sciences Naturelles de Belgique. Mémoires de l'Institut Royal des Sciences Naturelles de Belgique (2) 61:1–109.

Glibert, M. 1963. Les Muricacea et Buccinacea fossiles du Cénozoique étranger des collections de l'Institut Royal des Sciences Naturelles de Belgique. Mémoires de l'Institut Royal des Sciences Naturelles de Belgique (2) 74:1–179.

Glibert, M. 1973. Révision des Gastropoda du Danien et du

Montien de la Belgique. I. Les Gastropoda du Calcaire de Mons. Mémoires de l'Institut Royale des Sciences Naturelles de Belgique 173:1–116.

Golikov, A. N. and Y. I. Starobogatov. 1975. Systematics of prosobranch gastropods. Malacologia 15:105–232.

Grant, U. S. IV and H. R. Gale. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. Memoir of the San Diego Society of Natural History 1:1–1035.

Gray, J. E. 1857. Guide to the systematic distribution of Mollusca in the British Museum. Part 1. London, British Museum. 230 pp.

Herm, D. 1969. Mariner Pliozän und Pleistozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. Zitteliana 2:1–159.

Hertlein, L. G. and E. L Jordan. 1927. Paleontology of the Miocene of Lower California. Proceedings of the California Academy of Science (4)16:605–647.

Honda, Y. 1991. Paleogene molluscan biogeography of Japan. Saito Ho-On Kai Special Publication 3:489–506.

Honda, Y. 1994. History of the Paleogene molluscan fauna of Japan: a paleobiogeographic approach. Palaeogeography, Palaeoclimatology, Palaeoecology 108:295–309.

Ihering, H. von. 1907. Les mollusques fossiles du Tertiaire et du Cretacé supérieur de l'Argentine. Annales del Museo Nacional de Buenos Aires (Ser. III) 7:1–611.

Jung, P. 1974. Eocene mollusks from Curaçao, West Indies. Verhandlungen der Naturforschenden Gesellschaft Basel 84:483–500.

Jung, P. 1995. *Judaphos*, a new genus of buccinid gastropod from the Neogene of Costa Rica. The Veliger 38:43–46.

Kantor, Yu. 1991. On the morphology and relationships of some oliviform gastropods. Ruthenica 1:17–52.

Kantor, Yu. 1996. Phylogeny and relationships of Neogastropoda. Pp. 221–230 *In* J. D. Taylor, (ed.), Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, Oxford.

Kase, T. 1990. Late Cretaceous gastropods from the Izumi Group of southwest Japan. Journal of Paleontology 64: 563–578.

Keen, A. M. 1971. Seashells of Tropical West America. Palo Alto, Stanford University Press. 1064 pp.

Kensley, B. and J. Pether. 1986. Late Tertiary and Early Quaternary fossil Mollusca of the Hondeklip area, Cape Province, South Africa. Annals of the South African Museum 97:141–225.

Kilburn, R. N. 1989. A new genus and species of Pseudolivinae, with a note on the status of *Sylvanocochlis* Melvill, 1903 (Mollusca: Gastropoda: Olividae). Annals of the Natal Museum 30:177–184.

Kilburn, R. N. and A. J. Tankard. 1975. Pleistocene molluscs from the west and south coasts of the Cape Province, South Africa. Annals of the South African Museum 67: 183–226.

Koenen, A. von. 1889. Das Norddeutsche Unter-Oligocän und seine Mollusken-Fauna. Lieferung I: Strombidae-Muricidae-Buccinidae. Abhandlungen zur Geologischen Specialkarte von Preussen und den Thüringischen Staaten. Band 10. Berlin: J H Neumann 280 pp.

Kollmann, H. A., and J. S. Peel 1983. Paleocene gastropods from Nûgssuaq, West Greenland. Grönlands Geologiske Undersögelse Bulletin 146:1–115.

Kool, S. P. 1993. Phylogenetic analysis of the Rapaninae (Gastropoda: Muricidae). Malacologia 35:155–259.

Lussi, M. 1995. A new species of *Naudoliva* Kilburn, 1989 from off South Africa. World Shells (December, 1995):34–36.

Mansfield, W. C. 1925. Miocene gastropods and scaphopods from Trinidad, British West Indies. Proceedings of the United States National Museum 26(22):1–65.

Martin, K. 1914. Die Fauna des Obereocäns von Nanggulan, auf Java. Sammlungen des Geologischen Reichs-Museums in Leiden, Neue Folge 2 (4):107–178.

Melvill, J. C. 1903. The genera *Pseudoliva* and *Macron*. Journal of Conchology 10:320–330.

Mulliner, M. 1996. Dredging around Isla Danzante, Gulf of California, Mexico, or what you find at the end of a line. Festivus 28:62–70.

Muniz, G. de C. B. 1993. Novos Moluscos da Formação Gramame, Cretáceo Superior dos Estados de Paraíba e de Pernambuco, Nordeste do Brasil: com Dados Gerais Sobre a Formação e Revisão de Diversas Espécies Anteriormente Descritas. Recife, Universidade Federal de Pernambuco, Departamento de Geologia. 202 p.

Nagao, T. 1924. Occurrence of *Orthaulax* in the Paleogene of Japan. Japanese Journal of Geology and Geography 3:13–18.

Nagao, T. 1928. Paleogene fossils of the island of Kyûshû, Japan. Tohoku Imperial University Science Reports (2, Geology) 12:11–140.

Nelson, E. T. 1870. On the molluscan fauna of the later Tertiary of Peru. Transactions of the Connecticut Academy of Arts and Sciences 2:186–206.

Oleinik, A. E., and W. J. Zinsmeister. 1996. Paleocene diversification of bucciniform gastropods on Seymour Island, Antarctica. Journal of Paleontology 70: 923–934.

Olsson, A. A. 1928. Contributions to the Tertiary paleontology of northern Peru: Part 1, Eocene Mollusca and Brachiopoda. Bulletins of American Paleontology 14:47–154.

Olsson, A. A. 1930. Contributions to the Tertiary paleontology of northern Peru: Part 3, Eocene Mollusca. Bulletins of American Paleontology 17:1–96.

Olsson, A. A. 1932. Contributions to the Tertiary paleontology of northern Peru: Part 5, the Peruvian Miocene. Bulletins of American Paleontology 19:1–272.

Olsson, A. A. 1934. Contributions to the paleontology of northern Peru: The Cretaceous of the Amotape region. Bulletins of American Paleontology 20:1–104.

Olsson, A. A. 1964. Neogene mollusks from northwestern Ecuador. Ithaca, New York, Paleontological Research Institute. 256 pp.

Oppenheim, P. 1904. Über Tertiärfossilien, wahrscheinlich Eozänen Altes, von Kamerun. Beiträge zur Geologie von Kamerun, Band 3. Pp. 245–285. Stuttgart, Ernst Esch.

d'Orbigny, A. 1850. Prodrome de paléontologie stratigraphique universelle des animaux mollusques & rayonnés, faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques. Deuxiéme Volume. Paris, Victor Masson.

Palmer, K. V. W. 1937. The Claibornian Scaphopoda, Gastropoda and dibranchiate Cephalopoda of the southern United States. Bulletins of American Paleontology 7:1–548.

Palmer, K. V. W. and D. C. Brann. 1966. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Part II. Gastropoda. Bulletins of American Paleontology 48:471–1057.

Pervinquière, L. 1912. Études de paléontologie Tunisienne II. Gastropodes et lamellibranches des terrains Cretacés. Paris, Régents de Tunis, Protectorat Français, Direction Gé-

nérale des Travaux Publiques, Carte Géologique de la Tunisie. 352 pp.

Petuch, E. J. 1994. Atlas of Florida fossil shells (Pliocene and Pleistocene marine gastropods). Evanston, Illinois: Spectrum Press. 394 p.

Petuch, E. J. and D. M. Sargent. 1986. Atlas of the living olive shells of the world. Fort Lauderdale: Coastal Education and Research Foundation. 253 pp.

Peyrot, M. A. 1927. Conchologie néogénique de l'Aquitaine. Actes de la Société Linnéenne de Bordeaux 78:199–256.

Philippi, R. A. 1887. Die Tertiären und Quartären Verstemergungen Chiles. Leipzig, F. A Brockhaus. 266p.

Ponder, W. F. 1973. The origin and evolution of the Neogastropoda. Malacologia 12:295–338.

Ponder, W. F. and T. A. Darragh. 1975. The genus *Zemira* H. and A. Adams (Mollusca: Neogastropoda). Journal of the Malacological Society of Australia 3:89–105.

Ponder, W. F. and A. Warén. 1988. Classification of the Caenogastropoda and Heterostropha—A list of the family-group names and higher taxa. Malacological Review Supplement 4:288–326.

Quaas, A. 1902. Die Fauna der Overwegischichten und der Blätterthone in der Libyschen Wüste. Palaeontographica 30:153–336.

Ravn, J. P. J 1939. Études sur les mollusques du Paléocene de Copenhague. Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 1:1–106.

Riedel, F. 1994. Recognition of the superfamily Ficoidea Meek 1864 and definition of the Thalassocynidae fam. nov. (Gastropoda). Zoologische Jahrbucher, Abteilung fur Systematik, Geographie und Biologie der Tiere, 121:457–474.

Rossi Ronchetti, C. 1959. Revisione della fauna Neocretacica della Libia. Fam. Trochidae, Colombellinidae, Olividae. Rivista Italiana de Paleontologia e Stratigrafia 65:57–71.

Salvan, H. 1954. Les invertébrés fossiles des phosphates Marocains. Tome II: Paléontologie. Service Géologique, Maroc, Notes et Mémoires 93:1–257.

Smith, J. T. 1984. Miocene and Pliocene marine mollusks and preliminary correlations, Vizcaino Peninsula to Arroyo la Purisima, northwestern Baja California Sur, Mexico. In V. A Frizzell (ed.), Geology of the Baja California Peninsula. Pacific Section, Society of Economic Paleontologists and Mineralogists 39:197–217.

Sohl, N. F. 1964a. Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek, and Prairie Bluff Formations. United States Geological Survey Professional Paper 331-B:153–344.

Sohl, N. F. 1964b. Gastropods from the Coffee Sand (Upper Cretaceous) of Mississippi. United States Gaological Survey Professional Paper 331-C:345–394.

Sowerby, G. B. I 1846. Descriptions of Tertiary fossil shells from South America. In C. Darwin, Geological Observations on South America, being the Third Part of the Geology of the Voyage of the Beagle, Under the Command of Capt. Fitzroy, R.N., during the Years 1832 to 1836. London, Smith, Elder, and Company. pp. 249–264

Sowerby, G. B. I. 1859. Monograph of the genus *Pseudoliva*, Swains. Thesaurus Conchyliorum 3:73–75.

Squires, R. L. 1989. A new pseudolivine gastropod genus from the Lower Tertiary of North America. Journal of Paleontology 63:38–47.

Squires, R. L., W. J. Zinsmeister, and L. M. Paredes-Mejia. 1989. *Popenoeum*, a new pseudolivine gastropod genus,

widespread and most diversified during the Paleocene. Journal of Paleontology 63:212–217

Swainson, W. 1840. A treatise on Malacology; On the Natural Classification of Shells and Shellfish. London, Longman, Orme, Brown, Green, and Longmans. 419 pp.

Taylor, D. W. and N. F. Sohl. 1962 An outline of gastropod classificaiton. Malacologia 1:7–32.

Taylor, J. D., N. J Morris and C. N. Taylor. 1980. Food specialization and the evolution of predatory prosobranch gastropods. Paleontology 23:375–409.

Tessier, F. 1952. Contributions à la stratigraphie et à la paléontologie de la partie ouest du Sénégal (Cretacé et Tertiaire). Dakar, Imprimerie Africaine. 554 pp.

Thiele, J. 1929. Handbuch der Systematischen Weichtierkunde. Band 1 (1): Loricata; Gastropoda. Prosobranchia. Jena, Gustav Fischer. 376 pp.

Vermeij, G. J. 1995. Morphology and possible relationships of *Ecphora* (Cenozoic Gastropoda: Muricidae). The Nautilus 109.120–126.

Vermeij, G. J. 1997. The genus *Leucozonia* (Gastropoda: Fasciolariidae) in the Neogene of tropical America. Tulane Studies in Geology and Paleontology 29:129–134.

Vermeij, G. J. and S. P. Kool. 1994. Evolution of labral spines in *Acanthais*, new genus, and other rapanine muricid gastropods. The Veliger 37:414–424.

Vermeij, G. J. and T. J. DeVries. 1997. Taxonomic remarks on Cenozoic pseudolivid gastropods from South America. The Veliger 41: 23–28.

Vermeij, G. J and P. W. Signor. 1992. The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. Biological Journal of the Linnean Society 47:233–247.

Vermeij, G. J., and E. H. Vokes. 1997. Cenozic Muricidae of the western Atlantic region. Part XII—the subfamily Ocenebrinae (in part). Tulane Studies in Geology and Paleontology 29:69–118.

Vignon, P. 1931. Les dents du labre et les rapports qu'elles nonent avec les sillons, les cordons et les varices chez les gastéropodes. Journal de Conchyliologie 75:242–272.

Villatte, J. 1970. Deux Olividae identiques: *Pseudoliva prima* (Defrance) et *Pseudoliva pursanensis* Doncieux. Bulletin de la Société d'Histoire Naturelle de Toulouse 106:22–27.

Vokes, E. H. 1990. Cenozoic Muricidae of the western Atlantic region Part VIII—*Murex s.s.*, *Haustellum*, *Chicoreus*, and *Hexaplex*; additions and corrections. Tulane Studies in Geology and Paleontology 23: 1–96.

Vokes, E. H. 1992. Cenozoic Muricidae of the western Atlantic region Part IX—*Pterynotus*, *Poirieria*, *Aspella*, *Dermomurex*, *Acanthotrophon*, *Acantholabia*, *Attiliosa*; additions and corrections. Tulane Studies in Geology and Paleontology 25: 1–108.

Vredenburg, E. 1922. Analysis of the Singu fauna founded on Rao Bahadur S. Sethu Rama Rau's collections. Records of the Geological Survey of India 53:331–342.

Wenz, W. 1938–44. Gastropoda. Teil I: Allgemeiner und Prosobranchia. Handbuch der Paläozoologie 6. Berlin, Borntraeger.

Woodring, W. P. 1964 Geology and paleontology of Canal Zone and adjoining parts of Panama: description of Tertiary mollusks (gastropods: Columbellidae to Volutidae). United States Geological Survey Professional Paper 306-C:241–297.

Woods, H. 1922. Mollusca from the Eocene and Miocene deposits of Peru. In T. O. Bosworth (ed.), Geology of the

Tertiary and Quarternary periods in the north-west part of Peru. London, McMillan and Company, pp. 51–113.

Wrigley, A. 1941. New species of Eocene Mollusca from the Isle of Wight. Proceedings of the Malacological Society of London 24:161–168.

Zinsmeister, W. J. 1983. New Late Paleocene molluscs from the Simi Hills, Ventura County, California. Journal of Paleontology 57:1282–1303.

APPENDIX 1

Genera and species of Pseudolividae, together with a list of material examined for this study. The genus in which the species was described is given in parentheses if it differs from the genus to which it is assigned here.

Benthobia Dall, 1889

B. tryonii Dall 1889, type of genus: = *Nux alabaster* Barnard, 1960; *Lacuna cossmanni* Locard, 1897 (see Bouchet & Warén, 1985). **Distribution:** Recent, bathyal and abyssal western and eastern Atlantic, southwestern Indian Ocean, southwestern Pacific. **Material examined:** MNHN (Azores, Gulf of Mexico); USNM 717352 (Tulear, Madagascar), 824174 and 832910 (off Virginia).

Fulmentum Fischer, 1884

F. ancilla (Hanley, 1859) (*Pseudoliva*), type of *Sylvanocochlis* Melvill, 1903. **Distribution:** Recent, Agulhas Bank, South Africa.

F. sepimentum (Rang, 1832) (*Buccinum*), type of *Fulmentum*. **Distribution:** Recent, West Africa (Togo to Angola). **Material examined:** MNHN (Cotonou, Pointe Noire, Cap Esterias, Luanda); CAS 063185 (West Africa).

Fusopsis Ravn, 1939

F. canalifera (Ravn, 1939) (*Pseudoliva*), type of genus. **Distribution:** Paleocene, Copenhagen, Denmark.

Fusulculus Bouchet & Vermeij, 1997

F. albus Bouchet & Vermeij, 1997. **Distribution:** Recent, bathyal, New Caledonia and north of New Zealand. **Material examined:** MNHN.

F. crenatus Bouchet & Vermeij, 1997, type of genus. **Distribution:** Recent, bathyal, Coral Sea to northeast of Fiji. **Material examined:** MNHN (New Caledonia).

Hubachia Etayo Serna, 1979

H. ramirolobae Etayo Serna, 1979, type of genus. Distribution: Paleocene, Guajira, Colombia **Material examined:** UCMP 16014, 16105.

Luizia Douvillé, 1933

L. costae (Douvillé, 1933) (*Buccinum*), type of genus; = *L. costae* var. *brevis* (Douvillé, 1933). Distribution: Early? Miocene, Angola.

L. zebrina (A. Adams, 1855) (*Pseudoliva*). **Distribution:** Recent, Angola. **Material examined:** MNHN (Luanda, Moçamedes).

Macron H. & A. Adams, 1853

M. aethiops (Reeve, 1847) (*Buccinum*), = *Pseudoliva kellettii* A. Adams, 1855 (type of genus), *Purpura trochlea* Gray, 1839, *auct. non Buccinum trochlea* Bruguière, 1789;

? *Macron wrightii* H. Adams, 1865, ? *M. stereoglypta* Sowerby, 1882 (see Melvill, 1903). **Distribution:** middle Miocene (Olcese Sand), California; Pleistocene to Recent, Pacific coast of Baja California and Isla Danzante, Gulf of California (see Grant & Gale, 1931; Addicott, 1970; Mulliner, 1996). **Material examined:** GJV (Guerrero Negro); Mulliner collection (Isla Danzante); USNM 55665 (Cedros Island), 60074 (San Quentin Island), 60075 (San Quentin Bay), 102256 (Ballena Bay), 105428 (Scammons Lagoon), 105429 (Abreojos), 105432 (San Ignacio), 105433 (Manuel Lagoon), 105434 (Point Abreojos), 253114 (Lagoon Heads), 265240 (Cedros Island), 265601 (San Benito Island), 265613 and 265771 (Point Abreojos), 332389 (Magdalena Bay), 852828 (San Ignacio Lagoon), 1499926 (Gulf of California).

M. constrictus Gibson-Smith, Gibson-Smith & Vermeij, 1997. **Distribution:** early Miocene (Burdigalian, Cantaure Formation), Venezuela **Material examined:** NMB.

M. hartmanni Hertlein & Jordan, 1927. **Distribution:** middle to late Miocene (San Ignacio Formation), Baja California Sur, Mexico. **Material examined:** CAS 61714.07.

M. lividus (A. Adams, 1855) (*Pseudoliva*), type of *Macroniscus* Thiele, 1929. **Distribution:** Pleistocene to Recent, southern California. **Material examined:** GJV (La Jolla).

M. mcleani Vermeij, 1997. **Distribution:** Recent, Gulf of California. **Material examined:** LACM 2812.

M. merriami Arnold, 1907. **Distribution:** middle Miocene (Temblor Formation), California. **Material examined:** USNM 164982.

?*M. nipponensis* Chinzei, 1959. **Distribution:** Pliocene (Kubo Formation), Honshu, Japan.

M. orcutti Dall, 1918. **Distribution:** Pacific coast, Baja California Sur, Mexico. **Material examined:** LACM 79–26.27 (Punta Marquez), 71–3.26 (Punta Abreojos).

Naudoliva Kilburn, 1989

N. caitlinae Kilburn, 1989, type of genus. **Distribution:** Recent, Transkei, South Africa. **Material Examined:** NM E5750/T107.

N. guppyi (Mansfield, 1925) (*Pseudoliva*). **Distribution:** Late Miocene (Springvale Formation), Trinidad. **Material examined:** USNM 352664.

N. vorsteri Lussi, 1995. **Distribution:** Algoa Bay, South Africa **Material examined:** ANSP 399956.

Pseudoliva Swainson, 1840

P. crassa (Gmelin, 1791) (*Buccinum*), type of *Pseudoliva*; = *P. striatula* A. Adams, 1854 (see Melvill, 1903). **Distribution:** Recent, southern Angola. **Material examined:** MNHN (Baia dos Tigres, Ilha de Luanda); CAS 063184 (West Africa).

P. lutulenta Kensley & Pether, 1986. **Distribution:** early Pliocene (50-meter level), Hondeklip, Cape Province, South Africa = ? *P. crassa* (see text under *Pseudoliva*).

P. orbignyana Mayer, 1864. **Distribution:** Early? Miocene, Madeira.

Sulcobuccinum d'Orbigny, 1850

S. aaronsohni (Blanckenhorn, 1927) (*Pseudoliva*). **Distribution:** Late Cretaceous (Senonian), Palestine.

S. adelekei (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria. **Material examined:** USNM 174853.

S. ambiguum (Binkhorst, 1861) (*Pyrula*). **Distribution:** Late Cretaceous (Maastrichtian), Netherlands and ? Tunisia (see Pervinquière, 1912).

S. bellecomptum (Muniz, 1993) (*Pseudoliva*). **Distribution:** Late Cretaceous (Campanian) (Gramame Formation), northeastern Brazil.

S. bocaserpentis (Maury, 1912) (*Pseudoliva*). **Distribution:** Paleocene (Soldado Formation), Trinidad.

S. breve (Doncieux, 1908) (*Pseudoliva*). *Distribution:* Late Paleocene (Thanetian: Sparnacian), southern France.

S. briarti (Vincent, 1928) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium (see Glibert, 1973). **Material examined:** IRSNB 5467 (Mons) and unnumbered specimen (Ludanovka).

S. bussoni (Albanesi *in* Albanesi & Busson, 1974) (*Pseudoliva*). **Distribution:** Early Eocene (Series 6b), southern Tunisia.

S. carinatum (Conrad, 1860) (*Pseudoliva*). **Distribution:** Middle Eocene (Laredo, Stone City, Cook Mountain Formations, Archusa Marl), Gulf Coastal Plain (see Palmer & Brann, 1966; Dockery, 1980). **Material examined:** ANSP 7032.

S. chavani (Tessier, 1952) (*Pseudoliva*). **Distribution:** Paleocene (Marigot de Balling), Senegal.

S. coniforme (Oppenheim, 1904) (*Pseudoliva*). **Distribution:** Eocene, Cameroon.

S. coronaria (Olsson, 1930) (*Pseudoliva*). **Distribution:** Middle to Late Eocene (Saman and Talara Formations of Olsson, 1930), Peru. **Material examined:** PRI 24221.

S. cretaceum (Kase, 1990) (*Calorebama*). **Distribution:** Late Cretaceous (Late Campanian to Early Maastrichtian: Izumi Group), Japan.

S. curvicostatum (Briart & Cornet, 1870) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium (see Glibert, 1973). **Material examined:** IRSNB 5469, 5470.

S. dechordatum (White, 1887) (*Harpa*). **Distribution:** Paleocene (Maria Farinha Formation), Brazil, ? Early Paleocene (Marigot de Balling), Senegal (see Tessier, 1952). ? = *S. scalina* (see Palmer & Brann, 1966).

S. elegans (Hislop, 1860) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Intertrapine beds), Nagpur, India. **Material examined:** BMNH GS10297, 10298, 10299.

S. elisae (Briart & Cornet, 1870) (*Pseudoliva*), = *P. ludovicae, P. grossecostata,* and *P. elongata,* all of Briart & Cornet, 1870 (see Glibert, 1973). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium **Material examined:** IRSNB 5471–5474

S. eschi (Oppenheim, 1904) (*Pseudoliva*). **Distribution:** Eocene, Cameroon; ? Middle Eocene (Ameki Formation), Nigeria.

S. fischeri (Mayer-Eymar, 1887) (*Pseudoliva*). **Distribution:** Late Eocene (Bartonian), Thun, Switzerland.

S. fissuratum (Deshayes, 1835) (*Buccinum*), type of *Sulcobuccinum*. **Distribution:** Late Paleocene (Thanetian), Paris Basin, France. **Material examined:** MNHN (Chenay); RGM 58771 (Chenay).

S. funkeanum funkeanum (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria.

S. f. ornatum (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria.

S. guineense (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria. **Material examined:** USNM 174854, 174855.

S. howardi (Dickerson, 1914) (*Molopophorus*), type of *Pegocomptus* Zinsmeister, 1983; = *Pseudoliva reticulata* Waring, 1915 (see Zinsmeister, 1983). **Distribution:** Late Paleocene (Santa Susana and Sepultura Formations), southern California and Baja California. **Material examined:** LACM IP 22330, 22376, and 22688 (Santa Susana Formation, Simi Hills).

S. iminense (Moret, 1938) (*Pseudoliva*). **Distribution:** Paleocene, Sud-Atlas, Morocco (see Salvan, 1954).

S. japonicum (Nagao, 1924) (*Orthaulax*). **Distribution:** Late Eocene to Early Oligocene (Takashiman, Okinoshiman, Funazuan, and Mazean faunas), Kyushu, Japan (see Honda, 1991, 1994). **Material examined:** IGPS 8068, 8106, 35661 (Futago-Jima), 8069, 35660, 35684, 37769 (Hashima), 8105 (Shiratake), 35743 (Komenoyama), 36176 (Okinoshima), 36186 (Funazu), 36714 (Kiuragi).

S. kitsoni (Newton, 1922) (*Pseudoliva*). **Distribution:** Late Eocene (Ameki Formation), Nigeria (Eames, 1957). **Material examined:** BMNH G42069, 42062, 42070 to 42076.

S. koeneni (Ravn, 1939) (*Pseudoliva*), non *Purpura pusilla* Beyrich, 1854 (see Ravn, 1939). **Distribution:** Paleocene, Copenhagen, Denmark.

S. laudunense (Defrance, 1826) (*Buccinum*), = *Buccinum semicostatum* Deshayes, 1835. **Distribution:** Late Paleocene (Thanetian), Paris Basin, France (see Cossmann, 1889). **Material examined:** UCMP loc. B-5393 (Sinceny; MNHN (Pourcy).

S. leutweini (Böhm, 1926) (*Pseudoliva*). **Distribution:** Eocene, Namibia.

S. libycum (Quaas, 1902) (*Pseudoliva*). **Distribution:** Late Cretaceous (Maastrichtian), Egypt; Early Paleocene (Danian), East Tripoli, Libya

S. lineatum (Gabb, 1864) (*Pseudoliva*), = *P. dilleri* Dickerson, 1914 (type of *Calorebama* Squires, 1989), *Pseudoliva inornata* Dickerson, 1915, *P. kirbyi* Clark, 1938, *P. markleyensis* Clark, 1938, *P. tejonensis* Dickerson, 1915, *P. volutaeformis* Gabb, 1864 (see text under *Sulcobuccinum;* for different treatment see Squires, 1989). **Distribution:** Early to Late Eocene ("Meganos" to "Tejon" stages), Pacific North America. **Material examined:** UCMP 3679 (*P. dilleri*), 11053 (*P. inornatum*), 12472 (*P. markleyensis*), 15409 (*P. volutaeformis*), 15796 (*P. lineata*).

S. linosum (Conrad, 1860) (*Pseudoliva*), = *Pseudoliva moerens* de Gregorio, 1890 (see Palmer & Brann, 1966). **Distribution:** Middle Eocene (Weches, Stone City, and Cook Mountain Formations), Texas.

S. maritimum (Squires, Zinsmeister & Paredes-Mejia,

1989) (*Popenoeum*), type of *Popenoeum* Squires, Zinsmeister & Paredes-Mejia, 1989, = *Popenoeum maritimus bajaensis* Squires, Zinsmeister & Paredes-Mejia, 1989 (see text under *Sulcobuccinum*). **Distribution:** Paleocene (San Francisquito and Sepultura Formations), Baja California

S *michelini* Coquand, 1862, = *Pseudoliva michelini* vars. *longispinata, multispinata,* and *paucispinata,* all of Salvan, 1954. **Distribution:** Middle Eocene (Suessonian), North Africa (see Salvan, 1954).

S. *minutissimum* (Salvan, 1954) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Calcaire de Bonabont), Morocco.

S. *moabiticum* (Blanckenhorn, 1927) (*Pseudoliva*). **Distribution:** Late Cretaceous (Senonian), Palestine.

S. *multinodulosum* Vermeij, 1997, = *Pseudoliva chavani* Glibert, 1973, *non* Tessier, 1952 (see text under *Sulcobuccinum*). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium. **Material examined:** IRSNB 5368.

S. *mutabile douvillei* (Olsson, 1928) (*Pseudoliva*). **Distribution:** Early Eocene (basal Restin Formation), Peru. Material examined: PRI 3681.

S. *m. mutabile* (Woods, 1922) (*Pseudoliva*). **Distribution:** Early Eocene (lower Salina Group: Negritos Formation), Peru (see Woods, 1922; Olsson, 1928; Squires *et al.*, 1989).

S. *m. woodsi* (Olsson, 1928) (*Pseudoliva*). **Distribution:** Early Eocene (upper Salina Group: Negritos Formation), Peru (see Olsson, 1928; Squires *et al.*, 1989). **Material examined:** PRI 3684.

S. *nanafaliaense* (Aldrich, 1931) (*Pseudoliva*). **Distribution:** Early Eocene (Nanafalia Formation), Alabama.

S. *nanum* (Gardner, 1945) (*Pseudoliva*). **Distribution:** Paleocene (lower Midway Formation), Nuevo Leon, Mexico.

S. *obtusum* (Deshayes, 1835) (*Buccinum*), Deshayes, 1865 (see Cossmann, 1889). **Distribution:** Late Paleocene (Thanetian) and Middle Eocene (Lutetian), Paris Basin, France. **Material examined:** MNHN Sapicourt, Boisgeloup).

S. *ostrarupis ostrarupis* (Harris, 1896) (*Pseudoliva*). **Distribution:** Early Eocene (Bashi Marl Member, Hatchetigbee Formation), Alabama.

S. *s. pauper* (Harris, 1899) (*Pseudoliva*). **Distribution:** Early Eocene. Texas. **Material examined:** TMM BEG35590 and 35675

S. *perspectivum* (Conrad, 1860) (*Pseudoliva*). **Distribution:** Late Eocene (Moodys Branch Formation and Yazoo Clay), Mississippi. **Material examined:** GJV; MGS.

S. *praecursor* (Petbö, 1906) (*Pseudoliva*) **Distribution:** Late Cretaceous (Senonian), Hungary

S *primum* (Defrance, 1827) (*Struthiolaria*), = *Buccinum tiara* Deshayes, 1835, *Pseudoliva pursanensis* Doncieux, 1908, *P. binodosa* Traub, 1938 (see Villatte, 1970, Squires *et al.*, 1989). **Distribution:** Late Paleocene (Thanetian), Europe. **Material examined:** IRSNB (Noaille).

S. *pusillum* (Beyrich, 1854) (*Purpura*), = *Purpura nodulosa* Beyrich, 1854 (see Wrigley, 1941, and text under *Sulcobuccinum*). **Distribution:** Late Eocene (Priabonian: Lattorfian), northwestern Europe.

S. *retusum mancorense* (Olsson, 1928) (*Pseudoliva*) **Dis-**

tribution: Late Eocene (Chira, Mancora, and Heath Formations) and ? Early Oligocene, Peru. **Material examined:** PRI 3679, 3680.

S. r *retusum* (Philippi, 1887) (*Gastridium*), = *Pseudoliva parinasensis* Woods, 1922 (Vermeij & DeVries, 1997). **Distribution:** Early Eocene, Algarrobo, Chile; Early to Middle Eocene (Negritos and Talara beds of Olsson, 1928, 1930), Peru; as *Pseudoliva* sp. cf. *P. parinasensis*, Middle Eocene, Colombia (Clark & Durham, 1946). **Material examined:** SGO PI 765; UCMP 5020.

S. r. *samanicum* (Olsson, 1928) (*Pseudoliva*). **Distribution:** Middle to Late Eocene (Saman and Talara Formations of Olsson, 1928, 1930), Peru (= Verdun Formation), Peru; Late Eocene (Ceru Mainsjie), Curaçao (Jung, 1974). **Material examined:** PRI 3677, 3678, UCMP 35021, 35022 (Colombia).

S. *robustum* (Briart & Cornet, 1870) (*Pseudoliva*), = *Pseudoliva canaliculata* Briart & Cornet, 1870 (see Glibert, 1973). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium; ? Early Paleocene, Senegal (Tessier, 1952). **Material examined:** BMNH GS136, 8137, IRSNB 5466.

S. *rogersi* (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria.

S. *rosenkrantzi* (Traub, 1979) (*Pseudoliva*). **Distribution:** Late Paleocene (Oichinger Schichten), Austria.

S. *rude* (von Koenen, 1889) (*Pseudoliva*). **Distribution:** Late Eocene (Priabonian: Lattorfian), Germany

S. *santander* (Gardner, 1945) (*Pseudoliva*). **Distribution:** Late Paleocene to Early Eocene (Laredo, Tuscahoma, Wilcox, Hatchetigbee, and Nanafalia Formations), Gulf Coastal Plain of Mexico and the United States (see Dockery, 1980). **Material examined:** MGS (Bells Landing Member, Tuscahoma Formation).

S. *scalina* (Heilprin, 1881) (*Pseudoliva*). **Distribution:** Early Eocene (Nanafalia and Hatchetigbee Formations), Alabama ? = *dechordata* White, 1887 (see Palmer & Brann, 1966).

S. *schweinfurthi* (Oppenheim, 1904) (*Pseudoliva*). **Distribution:** Eocene, Cameroon.

S. *sofegginense* (Rossi Ronchetti, 1959) (*Pseudoliva*). **Distribution:** Late Cretaceous (Maastrichtian), East Tripoli, Libya.

S. *subcostatum paucicostatum* (Rossi Ronchetti, 1959) (*Pseudoliva*). **Distribution:** Late Cretaceous (Maastrichtian), East Tripoli, Libya.

S. s. *subcostatum* (Stoliczka, 1867) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Arrialoor beds), southern India.

S. *tenuicostatum* (Briart & Cornet, 1870) (*Pseudoliva*), = *Pseudoliva dubia* Briart & Cornet, 1870 (see Glibert, 1973). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium. **Material examined:** IRSNB 5475

S. *thielei* (Böhm, 1926) (*Pseudoliva*). **Distribution:** Eocene, Namibia. ? = *S. kitsoni* (see text under *Sulcobuccinum*).

S *tuberculiferum* (Conrad, 1860) (*Pseudoliva*). **Distribution:** Late Paleocene (Gregg's Landing and Bell's Landing Members, Tuscahoma Formation; Nanjemoy Formation) of Gulf and Atlantic coastal Plains

(see Squires, 1989). **Material examined:** MGS, UCMP loc. A-1056 (Bell's Landing Member).

S. unicarinatum (Aldrich, 1886) (*Pseudoliva*). **Distribution:** Early Paleocene (Matthew's Landing Member, Porters Creek Formation), Alabama (Squires, 1989). **Material examined:** MGS.

S. vetustum (Conrad, 1833), type of *Buccinorbis* Conrad, 1865; = *Monoceros fusiformis, M. pyruloides,* and *M. sulcatum,* all of Lea, 1833 (see Palmer, 1937). **Distribution:** Middle Eocene (Gosport Sand), Alabama. **Material examined:** GJV (Little Stave Creek), MGS.

S. vientoense (Clark & Durham, 1946) (*Pseudoliva*). **Distribution:** Eocene, Colombia. **Material examined:** UCMP 35023.

S. zittelli (Pethö, 1906) (*Pseudoliva*). **Distribution:** Late Cretaceous (Senonian), Hungary.

S. sp. aff. *S. maritimum* (*Pseudoliva*). **Distribution:** Paleocene (Sonja Member, Agatdal Formation), West Greenland (see Squires *et al.,* 1989; Kollmann & Peel, 1983).

S. sp. (as *Pseudoliva scalina* Heilprin, 1896, *non* Heilprin, 1881). **Distribution:** Early Paleocene (Clayton Member, Porters Creek Formation), Alabama (see Squires *et al.,* 1989).

S. sp. of Olsson, 1934 (*Pseudoliva*). *Distribution:* Late Cretaceous (Maastrichtian; Monte Grande Formation), Peru.

Sulcoliva Vermeij, 1997

S. modesta (Olsson, 1928) (*Pseudoliva*). **Distribution:** Late Eocene (Talara Formation of Olsson, 1930), Peru. **Material examined:** PRI 3668

S. monilis (Olsson, 1928) (*Pseudoliva*), type of genus. **Distribution:** Early Eocene (Parinas Sandstone and Restin Formation), Peru. **Material examined:** PRI 3671.

Testallium Vermeij & DeVries, 1997

T. cepa (Sowerby, 1846) (*Gastridium*), type of genus; = *Monoceros labiale* Hupé, 1854, *Fusus labialis* Hupé, 1854, *Monoceros opimum* Hupé, 1854, *Fusus opimus* Hupé, 1854, *Chorus sp.* aff. *C. blainvillei* of Watters & Fleming, 1972 (see Vermeij & DeVries, 1997). **Distribution:** Early Miocene (Navidad Formation and Punta Ahuenco beds), Chile; Early to Early Middle Miocene (Chilcatay and Pisco Formations), Peru. **Material examined:** BMNH G26399.

T. escalonia Vermeij & DeVries, 1997. **Distribution:** Late Pliocene (La Cueva Formation), Chile. **Material examined:** CAS 66500.01-.02; UCMP 39880.

T. voluta (Olsson, 1932) (*Acanthiza*). **Distribution:** Early Miocene (Heath Formation), Peru (see Vermeij & DeVries, 1997). **Material examined:** PRI 2302.

Triumphis Gray, 1857

T. distorta (Wood, 1828) (*Buccinum*), type of genus; = *Columbella triumphalis* Duclos, 1843 (Keen, 1971). **Distribution:** Recent, tropical eastern Pacific. **Material examined:** GJV (Costa Rica, Panama); USNM 368541 (Payta, Peru).

T. sp. of Addicott, 1970. **Distribution:** Middle Miocene (lower Olcese Sand), California.

Zemira H. & A. Adams, 1853

Z. australis antecursoria Ponder & Darragh, 1975. **Distribution:** Early Miocene (Longfordian and Batesfordian), Victoria, Australia.

Z. a. australis (G. B. Sowerby I, 1833) (*Eburna*), type of *Zemira* ; *Zemira praecursoria* Tate, 1888, *Eburnopsis aulacoessa* Tate, 1889 (Ponder & Darragh, 1975). **Distribution:** middle Miocene (Balcombian) to Recent, temperate Australia. **Material examined:** CAS 28597 (Victoria); USNM 130901 (Tanner, Chamberlain), 202777 and 203906 (Westernport).

Z. bodalla Garrard, 1966. **Distribution:** Recent, southern Queensland.

Z. tessellata Tate, 1893. **Distribution:** Jan Juc Formation (Late Oligocene), Victoria. **Material examined:** IRSNB (Spring Hill).

Z. sp. of Ponder & Darragh, 1975. **Distribution:** Glen Aire Clay (Late Eocene), Nigeria. **Material examined:** RGM (Bende).

APPENDIX 2

Material examined of some species belonging to neogastropod families other than Pseudolividae.

Family Olividae, subfamily Ancillinae

Baryspira australis (Sowerby, 1830): GJV (Leigh, New Zealand)

Eburna glabrata (Linnaeus, 1758): GJV (near Punto Fijo, Venezuela)

Family Strepturidae

Melapium lineatum (Lamarck, 1822): USNM 687845 and 609711 (Jeffreys Bay, South Africa)

Strepsidura turgida (Solander *in* Brander, 1766): UCMP Localities B-5357 (Cressay, Late Eocene), B-5404 (Fleury-la-Riviére, Middle Eocene), B-5402 (Herouval, Late Eocene), B-6484 (Levignen, Late Eocene), all Paris Basin, France.

Family Buccinidae, subfamily Photinae

Cominella acutinodosa (Reeve, 1846): USNM 691693 and 691707 (Bandicoot Bay, Barrow Island, Western Australia)

Iosepha glandiformis (Reeve, 1847): GJV (several localities near Leigh and Dunedin, New Zealand)

I. tasmanica Tenison-Woods, 1878: USNM 638596 (Dunsborough, Western Australia)

Nicema amara Woodring, 1964: USNM 243665 (lower Gatun Formation, Panama)

N. noctua (Olsson, 1964): USNM 644018 and 645271 (Angostura Formation, Ecuador, Late Miocene)

N. solida (Nelson, 1870): YPM 00507 (Cardalitos beds, Peru, Late Miocene; see Vermeij & DeVries, 1997)

N. subrostrata (Wood, 1828): GJV (San Blas, Mexico)

N. venada (Olsson, 1964): USNM 644019 (Rio Cayapas, Ecuador; Late Miocene)

Family Melongenidae, subfamily Echinofulgurinae

Cornulina minax (Solander *in* Brander, 1766): MNHN (Late Eocene, Paris Basin); UCMP Locality B-5356 (Crenes, France; Middle Eocene).

Protobusycon cretaceum (Wade, 1917): USNM 32897
    (Coon Creek, Tennessee; Late Cretaceous: Maas-
    trichtian)

Families uncertain

Hydrotribulus elegans Sohl, 1964: MGS (Coon Creek,
    Tennessee; Late Cretaceous: Maastrichtian) *nodosus*
    Wade, 1916: USNM 32915 and 130456 (Coon Creek,
    Tennessee; Late Cretaceous: Maastrichtian)
Laccinum lugardi (Newton, 1922): RGM (Ameki For-
    mation, Late Eocene, Nigeria)

Lacinia alveata (Conrad, 1833): GJV, UCMP Loc. A-959
    (Gosport Sand, Middle Eocene, Alabama)
Ptychosyca inornata (Gabb, 1876): USNM 13454 and
    13455 (Ripley Formation, Late Cretaceous (Maas-
    trichtian) of Tippah County, Mississippi)
Seymourosphaera bulloides Oleinik & Zinsmeister, 1996:
    PU Localities 1136, 1430, 1501 (*S. bulloides*); 9 (*S.
    depressa*); 1434 and 1435 (*S. subglobosa*); 1328 and
    1138 (*S. elevata*) (all names of Oleinik & Zinsmeis-
    ter, 1996), all Paleocene of Seymour Island, Antarc-
    tica.